VERNALIZATION

and

PHOTOPERIODISM

A SYMPOSIUM

by A. E. MURNEEK *and* R. O. WHYTE

with H. A. ALLARD, H. A. BORTHWICK, ERWIN BÜNNING, G. L. FUNKE, KARL C. HAMNER, S. B. HENDRICKS, A. LANG, M. Y. NUTTONSON, M. W. PARKER, R. H. ROBERTS, S. M. SIRCAR, B. ESTHER STRUCKMEYER and F. W. WENT

Foreword by KENNETH V. THIMANN

WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

Marine Biological Laboratory

Received July 19, 1958

Accession No. 73772

Given By Ronald Press Company
New York City

Place,

MBL/WHOI
0 0301 0014366 5

The Chronica Botanica Co., International Plant Science Publishers

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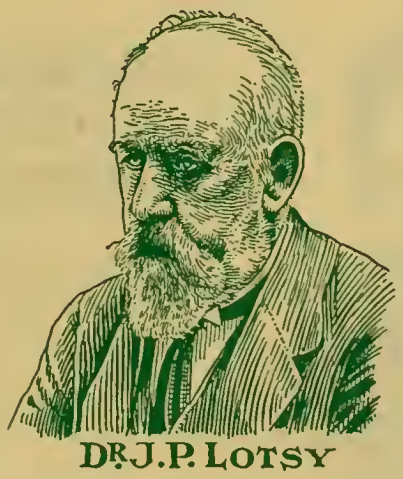
• LOTSYA — A BIOLOGICAL MISCELLANY •

Edited by Frans Verdoorn — Volume 1



VERNALIZATION

and

PHOTOPERIODISM

Т. Д. ЛЫСЕНКО

ТЕОРЕТИЧЕСКИЕ ОСНОВЫ ЯРОВИЗАЦИИ

1935
ГОСУДАРСТВЕННОЕ ИЗДАТЕЛЬСТВО
КОЛХОЗНОЙ И СОВХОЗНОЙ ЛИТЕРАТУРЫ
МОСКВА—ЛЕНИНГРАД

FRONTISPIECE (wood cut portrait of the author) and TITLE PAGE OF LYSENKO'S *Theoretical Bases of Vernalization* (1935), *see* pp. 5-8.

LYSENKO, whose name is identified so closely with the early practice of vernalization, "is an excellent prophet," writes ASHBY in his recent 'Scientist in Russia': "He is full of the unquenchable optimism, the impatience with inactivity, the scorn of the word 'impossible,' which Russia must have to complete her social experiment. He is a peasant who understands peasants. He is a shrewd and clever practical agriculturist . . . When potato yields were too low in the Ukraine, he suggested that tubers should be sown in summer instead of spring. . . When he saw the thin layers of snow being driven by winds off the fields in Siberia, he shocked convention by announcing that wheat should be sown in stubble. Again it worked. When the much-advertised pre-treatment of grain by low temperatures . . . proved a great failure, LYSENKO cleverly substituted another pre-treatment which is virtually a germination test, but which appeared under his name in the decrees for the Spring sowing in 1945 and 1946. He is the peasants' demagogue. What he says to them, goes. And he epitomises dialectical materialism in action; he provides the practical philosophy for the collective farm. If the Bolsheviks had not believed that man can remake his crops, his beasts, and even himself, they would not be where they are today. The missionaries of this faith have to be less sophisticated than the average polished and well-educated Academician. That, in my opinion, is one reason why LYSENKO and his school are quietly tolerated."

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WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

First published MCMXLVIII
By the Chronica Botanica Company
of Waltham, Mass., U. S. A.

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FOREWORD

It is an honor to be asked to contribute a foreword to this stimulating publication. The book, of course, owes its inception to Dr. VERDOORN's enthusiastic interest in the documentation of plant science. As a matter of history, it is the last of a series of titles which were originally announced by him before the war and have one by one been published during the last seven years. The authors of these chapters have cooperated generously and have produced conscientious and thorough reviews of their several fields. They are authoritative and familiar with the ramifications of the work they discuss. One of them is himself the author of a book in the same general field.[1] At the moment, therefore, these comprise almost the last word.

Nevertheless, although the present seems a particularly opportune moment for the appearance of this book, there can be no doubt that in this field, which is developing so rapidly, fundamental changes in outlook might well come at any moment. Such a highly flexible situation is of course typical of experimental plant science, which in many respects is still somewhat embryonic, but it is perhaps particularly so of the branches of plant physiology and agronomy which are discussed here.

The reasons for this are basically simple. The physiology of flowering, with which this book deals, has as yet no basis in the general physiology and biochemistry of the plant. The fundamental discoveries on which it rests are the effects of the chilling of germinating seeds, and of the varying of the length of day in mature plants approaching the stage of "readiness to flower (Blühreife)". Both of these are essentially *ad hoc* discoveries which did not arise directly from a continuing chain of closely-knit research and deduction, such as, for instance, that on which genetics rests today, or even that which led to our rather extensive knowledge of the auxins. They have inspired a large amount of experiment and have led to very important practical applications in the agriculture of both temperate and tropical zones, which are discussed in the several chapters of this book. But the underlying problems are difficult to attack and, indeed, it is not quite clear that they can even be formulated. What, for instance, is the nature of the change from the vegetative to the flowering state? Is it localized in the buds themselves, as would be implied by the concept of a flowering hormone, of which the buds would be the receptors, or is it systemic—a symptom of an inner complete change in metabolism, as in the theory of phasic development? Curiously enough, these two viewpoints have each become associated with one of the two main fields of endeavor, namely photoperiodism and vernalization respectively.

Only recently have these two basic ideas shown signs of approaching one another. It should be pointed out that the demonstration by GREGORY

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[1] WHYTE, R. O., Crop Production and Environment (London: Faber & Faber), 1946, 372 p. For the sake of completeness the following recent book may also be mentioned: DAVID, R., Facteurs de développement et printanisation des végétaux cultivés (Paris: Hermann et Cie.), 1946, 177 p.

and PURVIS that vernalization of cereals may be reversed points in the general direction of control by special substances rather than by the successive completion of determinative "phases." However, it is important to note that SEN and CHAKRAVARTI[2] have been unable to reverse the vernalization of mustard either by high temperature or by dry storage for a year. Mustard differs, however, from rye in that the excised embryos can be fully vernalized in pure water, while rye embryos require sugar for complete and rapid vernalization. Whether there is any connection between this need for carbohydrate and the reversibility of vernalization is, of course, not known yet. However, the metabolism which accompanies vernalization may well be worth analysis. Indeed, the way may have been opened to such an analysis by the recent experiments of PURVIS[3], which indicate that, during a period of starvation of the rye embryo, some materials necessary not only for vernalization but also for growth are metabolized away. Perhaps at this point our developing knowledge of the special nutritional requirements of young embryos in culture may be brought to bear. A very recent paper by LANG and MELCHERS,[4] unfortunately received too late for inclusion in the text, brings the two ideas together in another way. Biennial *Hyoscyamus niger,* which flowers after vernalization only if kept in long days, can be devernalized if given ten short days at 38°. This treatment must, however, be applied immediately (within four days) after the vernalization by cold. Thus the flowering condition or substance is destroyed before it has had time to act. Another recent piece of evidence strongly suggestive of the former, or hormonal view, is supplied by HOLDSWORTH and NUTMAN'S[5] study of the flowering of *Orobanche.* This parasite evidently initiates flowers only when its host, red clover, does so; in other words, the receptors for the flowering "hormone," whose production depends on day-length, are not only the buds of the host but also those of the parasite. The formation and destruction of special substances, or alternatively the balance between their production and its inhibition, is, of course, the general line of interpretation adopted by the workers in photoperiodism. The former of the two alternatives is essentially that of HAMNER and of BORTHWICK, PARKER and their co-workers at Beltsville, the latter that of MELCHERS and his collaborators. It is needless to add, however, that the nature of these hypothetical substances and the metabolic conditions under which they are produced remain completely unknown. Nevertheless, this vast hiatus does not at present interfere seriously with the development of the field, since these ideas are little more than interpretations and are not specifically formulated theories which can stand or fall by experiments designed to test them.

Another group of questions which we are perhaps not yet ready to formulate concerns the mode of action of the stimulus (or the substances). In the case of vernalization of the grasses the impetus to flower formation seems to appear as a change in the primary meristem; in the dicotyledons the contribution of ROBERTS and STRUCKMEYER suggests that it may be the secondary meristem which shows the initial and determining responses.

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[2] SEN, B. and CHAKRAVARTI, S. C. *in* Nature 157 : 266, 1946; 159: 783-4, 1947.

[3] PURVIS, O. N. *in* Ann. Bot. N.S. 11: 269-283, 1947.

[4] LANG, A. and MELCHERS, G. *in* Zeit. Naturforsch. 2b: 444-449, 1947 (received May 1948).

[5] HOLDSWORTH, H. and NUTMAN, P. S. *in* Nature 160: 223, 1947.

Harry Ardell Allard (*b.* 1880), formerly Senior Physiologist, Div. of Tobacco Investigations, Bureau of Plant Industry Station, U. S. Dept. of Agriculture, retired since Sept. 1946.

Anton Hendrik Blaauw (17 Sept. 1882-11 Nov. 1942), for many years Professor of Plant Physiology, College of Agriculture, Wageningen, the Netherlands. Frontispiece of W. H. Arisz's biography in Jaarb. Nederl. Akad. Wetensch. 1941/42.

Wightman Wells Garner (*b.* 1875), formerly Principal Plant Physiologist, Div. of Tobacco Investigations, Bureau of Plant Industry Station of the U. S. Dept. of Agriculture, Beltsville, Maryland.

Nikolaj Grigorjevich Cholodny (*b.* 1882), Ukrainian plant physiologist, who survived the war years and continues his work at Kiev.—After a painting by Streblov (based on a photograph), *courtesy of Mrs. Harvey.*

GUSTAV GASSNER (*b.* 1881), German plant physiologist who was forced to go abroad and became Director, Central Institute of Plant Pathology in Ankara; now Rector, College of Technology, Braunschweig.—After a painting by FRED HARDING (based on a photograph), *courtesy Univ. of Minnesota.*

GEORG KLEBS (23 Oct. 1857-15 Oct. 1918), the great German plant physiologist and experimental morphologist, longtime Professor of Plant Physiology at the Univ. of Heidelberg.—After a painting by FRED HARDING (based on a photograph), *courtesy Univ. of Minnesota.*

T. D. LYSENKO (*b.* 1898), the well-known Russian agronomist.—After a painting by FRED HARDING (based on a photograph), *courtesy Univ. of Minnesota.*

NIKOLAJ ALEXANDROVICH MAXIMOV (*b.* 1880), the distinguished Russian plant physiologist, after a painting by STREBLOV (based on a photograph), *courtesy of Mrs. Harvey.*

If it be the meristems which are initially changed, then the subsequent reactions leading to flowering may result from differences in the supply system and therefore in the materials made available to the developing initials. Similar effects exerted through the transporting system may be operative in the thermoperiodic phenomena described by WENT.

Some of the questions are less broad and are susceptible of immediate attack. One of these is the nature of the photo-receptor pigment, the measurement of whose absorption spectrum by the Beltsville group is described in one of the following chapters. Another is the role of sugar-feeding and induced fermentation studied by MELCHERS, LANG and CLAES, and discussed in the articles by MURNEEK and HAMNER. Still another is the relation of auxin production to flowering; it is a striking fact that, in pineapple, auxin greatly hastens flowering, while in other plants its effect tends to be in the opposite direction. Indeed, GALSTON[6] has ascribed the effect of triiodobenzoic acid in increasing the number of flower-buds in soybeans to the antagonistic effect of this substance on the auxin of the plant. The reduction of cambial activity preceding flowering in the plants studied by ROBERTS and STRUCKMEYER would also indicate an opposition between auxin and flowering. The very rapid reactions to change in day-length in such plants as the soybean, of course, would not suggest that such cambial changes were causative in themselves, but they could certainly be an indication of decreased auxin production. Very recently, both THURLOW and BONNER[7] and LEOPOLD[8] have found, using different plants and different methods, that auxin, applied externally, may inhibit to some extent the normal process of flowering. A number of older observations, both botanical and horticultural, point in the same direction, while the peculiar and (at present) isolated case of pineapple, whose flowering is promoted by auxin, cannot be overlooked. Whether auxin plays a major role in the flowering process, however, (either as a promoter or an inhibitor), is far from established, though there is doubtless an interesting avenue here to be opened up. A more extensive discussion of this phase of the problem has been given elsewhere.[9]

It may be, and this is undoubtedly the usual course of research, that further study of these more concrete problems will lead to a gradual elucidation of the broader and more intangible unknowns. But as was stated at the outset, the state of the field is such that a single clear-cut result might change its whole aspect almost overnight.

The consequences of major progress in this area are very great, not only for pure science but for agriculture. In these days when so much of the world is near to starvation no worker can fail to carry this thought in the back of his mind, in spite of the frequent statement that research is its own reward and that no further incentive is necessary. One purpose of a symposium like the present publication is to enable the individual student to effect something of a synthesis in his views. Such a synthesis can hardly fail to engender new ideas and thus to quicken the pace of progress.

KENNETH V. THIMANN
Harvard University

[6] GALSTON, A. W. *in* Amer. J. Bot. 34:356-360, 1947.
[7] THURLOW, J. and BONNER, J. (Abstr.) *in* Amer. J. Bot. 34: 603, 1947.
[8] Unpublished data.
[9] THIMANN, K. V. *in* The Physiology and Chemistry of Hormones, Chapter 3 (New York: The Academic Press), 1948.

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VERNALIZATION

OR

Lyssenko's Method for the Pre-treatment of Seed

BY

R. O. WHYTE, PH.D. and P. S. HUDSON, PH.D.

(Bulletin No. 9 of the Imperial Bureau of Plant Genetics, Herbage Plants and Occasional publication of the Imperial Bureau of Plant Genetics, for plants other than herbage.)

Published by the
IMPERIAL BUREAUX OF PLANT GENETICS,
Aberystwyth and Cambridge,
Great Britain.

Price 2/6.

March. 1933.

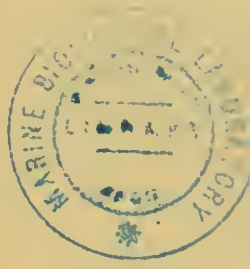
TITLE PAGE OF WHYTE AND HUDSON'S ACCOUNT OF LYSENKO'S VERNALIZATION METHOD (1933)

HISTORY OF RESEARCH IN VERNALIZATION

by

R. O. WHYTE

Commonwealth Bureau of Pastures and Field Crops, Aberystwyth



Introduction: — It requires to be stressed at the outset that the treatment and responses associated with the term "vernalization" represent only one aspect of the work on the developmental physiology of plants, which is receiving the attention of many research workers at the present time. Research on developmental physiology may be said to have begun with the experiments of KLEBS in the years up to about 1918. Earlier experiments had been made, but KLEBS may be regarded as the initiator of the modern extension of this branch of plant physiology, the main thesis of which is that it should be possible to control and direct the processes of growth and development of a plant by exposure under artificial experimental conditions to the particular factors of environment to which it is exposed in the cultivated field or greenhouse or in nature.

In this research on developmental physiology, reviewed by the author elsewhere (WHYTE, 1946), it appears that the decisive factors of the environment which control growth and development are temperature and light (its presence or absence), and that, once these factors have had an opportunity of operating to the required degree, a further set of conditions, including such factors as the relationship between carbohydrate and nitrogen, water relations, general nutrition and so on, then operate and determine whether a plant shall ultimately exhibit vegetative growth or reproduction (development).

A plant displays the capacity to respond to the temperature of its environment in certain instances remarkably soon after fertilization, within 5 or 6 days in one case studied. This capacity is progressively lost with approaching dormancy, and is reacquired when dormancy of the ripe seed is broken and germination begins. As soon as chlorophyll is formed in the leaves of the young seedling, the light régime of the environment can begin to operate, and from then on the behaviour of a plant appears to depend upon the interrelationship of these two factors, temperature and light. Plants such as winter cereals proceed most rapidly to reproduction if they are first exposed to a certain quota of low temperature, followed by an exposure to a sufficient number of days of the appropriate length, together with an optimal temperature.

The terms of reference of this article limit consideration to the acquisition by germinating seeds or young seedlings, either in their natural environment or under experimental conditions, of that particular dose of low temperature under the influence of which they can proceed most rapidly and efficiently to reproduction, provided the environment to which they are subsequently exposed is optimal for the reproductive processes of that variety. It is therefore necessary to ignore the wider questions relating to the effect of temperatures at all stages of a plant's life on its reproductive behaviour. The effect of temperature on the photoperiodic reaction of plants is being discussed by MURNEEK (pages 39 *et seq.*). From investigations of plant growth and development such as those being conducted by WENT at the California Institute of Technology, Pasadena (1943, 1944*a*, 1944*b*), a much fuller understanding of the significance of temperature will be forthcoming; using air-conditioned greenhouses, it is now possible to maintain the total environment under control throughout the life of a plant, from fertilization to seed formation.

Taking again the example of *winter* cereals in the latitudes in which they are cultivated, it has long been the practice to arrange their sowing dates in such a way that they are exposed while in the field to the low temperatures desirable, but apparently not obligatory, for progress to reproduction. If these varieties are sown in spring alongside the spring varieties, differentiation of flower primordia may occur after a considerable period of time, but earing does not occur normally. It was the aim of the chillers of

seed to give such grain their specific quota of low temperature in the laboratory or the barn and to sow them in the spring in the hope that they would come into ear in the same season, that is, they would behave like spring varieties, although not, as some have erroneously stated, to the extent of being "converted" into spring varieties.

GASSNER (1918) was one of the early chillers of grain, giving cereals in the laboratory the dose of low temperature they would normally receive in the field after being sown in the autumn in Germany. His work is discussed later. In subsequent years others chilled various types of seeds, but the interest of agricultural physiologists became transferred to the relations between light and development and particularly to the work of GARNER and ALLARD and their successors on the photoperiodic reactions and categories of plants.

The interest in temperature was, however, revived and the attention given to developmental physiology as a whole stimulated by the elaboration by LYSENKO and his associates at the Institute of Plant Breeding and Genetics, Odessa, of the technique which has come to be known throughout the English-speaking world as vernalization. This technique is considered by the Russians to differ from that of GASSNER in recognizing that only a minimum of growth is essential during low temperature exposure so that development can take place.

The theoretical principles which were elaborated from the experimental data quickly exerted a revolutionary effect on the whole trend of Soviet research in plant biology, expressed in a spate of scientific and agronomic articles dealing with theory and practical applications.

Largely through the medium of the publications of the Imperial Agricultural Bureaux (1933, 1935), this technique and the theoretical principles were made available to English-speaking readers, and this was followed by many experiments on the vernalization of a wide range of crops under a wide range of environments. The technique was regarded as the solution of the problem of bringing crops to maturity in the short Northern summer and of producing crops in drought-affected regions, of bringing high cash value crops such as market garden or greenhouse plants to maturity in time to catch early markets, or of producing seed in one year from biennial or perennial crops not normally fruiting in their first year. It must be admitted that this was a period of dogmatic assertions and exaggerated or ill-founded claims, of uncertain techniques and an incomplete understanding of the fundamental biological principles. That period is now past and it is therefore appropriate to review its consequences, and to examine the changes in scientific knowledge and agricultural or horticultural practice which have been achieved.

It will be convenient to deal with this by using a combination of the historical and geographical approaches, thus indicating the international nature of the problems and how investigators in many different countries have been tackling them. In the U. S. S. R., where the technique of vernalization had its origin, the emphasis throughout has naturally been on the applied and practical results to be obtained from its use. After the "fashion" created by the I. A. B. publications had died down, the nature of the interest in countries outside the U.S.S.R. has varied considerably. In Germany it was primarily practical, concerned with its use in making possible the cultivation of such only partially adapted crops as the soybean. Interest in India is both academic and practical, the latter to the extent that centres for vernalization of crop seeds have been suggested, in order to supply cultivators with properly treated seed which, when sown, would produce plants which would reach maturity more rapidly than those from untreated seed and thus avoid a period of adverse environment such as excessive heat, drought or floods.

In Great Britain, on the other hand, research has been concerned primarily with the fundamental biological processes underlying the technique of vernalization. The work of F. G. GREGORY, O. N. PURVIS and others of the Research Institute of Plant Physiology of the Imperial College of Science and Technology, South Kensington has provided an important analysis of the causal factors in this reaction to temperature treatment. The historical trend of these experiments is reviewed later.

Chilling of Seed: — Many reviewers have suggested that there is nothing new in the vernalization technique. MCKINNEY (1940) has

brought into prominence a little of this historical background, stating that "it seems only fair to point out that the basic concepts involved in these studies (on vernalization and developmental phases) have been known within certain circles for many years. They simply have not been recognized in all circles of plant science until recently." After stating that the older horticultural and agricultural journals and the older scientific journals and text books demonstrate that some growers and some botanists had already recognized part or all of these concepts, McKinney refers to an early report in 1857 by Klippart of Ohio, and even earlier records (20 years before Klippart) of the production of a crop of grain from spring-sown winter-wheat seed which had been subjected to low temperatures before sowing. Klippart's statement is so much to the point that it is again quoted here from McKinney.

"To convert winter into spring wheat, nothing more is necessary than that the winter wheat should be allowed to germinate slightly in the fall or winter, but kept from vegetation by a low temperature or freezing, until it can be sown in the spring. This is usually done by soaking and sprouting the seed, and freezing it while in this state and keeping it frozen until the season for spring sowing has arrived. Only two things seem requisite, germination and freezing. It is probable that winter wheat sown in the fall, so late as only to germinate in the earth, without coming up, would produce a grain which would be a spring wheat, if sown in April instead of September. The experiment of converting winter wheat into spring wheat has met with great success. It retains many of its primitive winter wheat qualities, and produces at the rate of 28 bushels per acre."

From these and similar examples, one can bring the discussion into modern times by reference to the classic experiments of Klebs and Gassner which, as already noted, provided the starting point of the modern branch of biological research concerned with developmental physiology.

The work of Klebs was concerned with the control of growth and development by appropriate adjustments of the decisive factors of the environment, temperature and light. Three developmental phases were recognized, not all of the same nature. Ripeness-to-flower is a qualitative phase not recognizable morphologically, and is dependent on the temperature effect in relation to assimilation and dissimilation. The initiation of flower primordia and the formation of inflorescences and flowers are quantitative phases, recognizable morphologically. This research by Klebs and the postulation of a form of phasic development contain at least a reference to most of the problems at issue in the study of the developmental processes in plants, and of the reasons for the transformation from a vegetative to a reproductive state. He recognized the effect of the decisive factors, temperature, light and/or darkness, alone or in combination, upon a series of phases or conditions, each one of which must be established before the next can begin; a hint of an after-effect of light treatment; evidence of reversal of development; the internal metabolic changes associated with vegetative growth or reproductive development.

Klebs was, however, primarily concerned with the effect of light. Gassner (1918) was primarily interested in temperature, and temperature only in the early stages of plant growth, just after germination. As Gassner considered that the shooting and flowering of winter cereals depends to a marked degree on their passing through a period of low temperature, ex-

periments were conducted with the following objects: — to determine (*1*) the principles underlying the effect of low temperatures on flower production, and (*2*) further details regarding (*a*) co-operation of the temperature of germination, and temperature and other conditions during the course of vegetation, and (*b*) the significance of the vegetative period in understanding the relative peculiarities of summer and winter cereals.

GASSNER sowed the seed of cereals in sand at different dates between January 10th and July 3rd, and subjected them to the following temperatures during germination: 1 to 2°, 5 to 6°, 12° and 24°C. Selected seedlings were subsequently placed in pots and then planted out. Tables and graphs in his paper show (*a*) date of sowing, (*b*) temperature during germination, (*c*) "appearance above ground," when the young leaf had reached a length of 20 to 25 mm., and (*d*) shooting. The crop plants used were Petkus winter rye and Petkus spring rye. The results may be summarized as follows (GASSNER, 1918):

The temperature during germination had no influence on shooting of spring rye; plants germinated at the temperatures quoted above, all shooting at regular and uniform intervals. In winter rye, only the plants germinated at 1 to 2°C. exhibited shooting regularly throughout the whole vegetative period. Plants germinated at 5 to 6°C. only shot regularly if their "appearance above ground" had occurred before the end of April, and those germinated at 12° and 24°C. only if they had appeared above ground before the middle of April and the end of March respectively.

Some plants did not shoot at all, but of those which did, the plants that had appeared above ground simultaneously attained shooting all the sooner, the lower the temperature at which they had been germinated. Thus, plants which appeared above ground in the middle of March and which had been germinated at 1 to 2°C. shot about 9 days, 21 days and 41 days earlier than those that had been germinated at 5 to 6°C., 12°C., and 24°C. respectively. The illustrations in GASSNER's article indicate the further difference that plants germinated at a low temperature not only reached the shooting stage more rapidly but also more regularly than those germinated at a higher temperature.

GASSNER's conclusions regarding the physiological difference between spring and winter rye were as follows: Spring rye is practically independent of any need to pass through a cold period before it can achieve shooting (Blütenauslösung). The flowering (Blütenbildung) of winter rye depends on its passing through a cold period either during germination or at some stage subsequent to germination.

GASSNER made some observations regarding the correlation between winterhardiness, sugar content and flowering. Without going into any great detail with regard to the problem of death of the plant cell through cold, he stated that the following may be quoted as definite facts:

(1) The growing of winter plants at a low temperature induces increased winterhardiness;

(2) low temperature is a condition for the "release of flower formation;"

(3) cultivation at low temperature increases sugar content; it may be assumed that winterhardiness and sugar content are in a causal relationship, while the "release of flower formation" depends on sugar content;

(4) winterhardiness and the cold-requirement, so important for flowering, are correlatively connected.

It can thus be seen that, in the period before the technique of vernalization was evolved and received such publicity, research workers in several countries were concerned with this type of study and had proceeded a certain distance in the direction of controlling growth and development by the manipulation of the environment. Progress was being made in the Soviet Union as well, where MAXIMOV continued the experiments of GASSNER and treated seedlings with low temperature, thereby influencing the whole of their further development. Winter cereals which, when sown in spring, did not normally reach the heading stage, headed and flowered normally when the seedlings had been exposed to a short period of chilling. It was found possible to direct or determine the further course of development by treating them during the early stages of growth with appropriate temperatures and a given periodicity of light. Although these experiments provided a basis for understanding the behaviour of winter varieties in the field when sown in autumn in the normal way, the technique was still, however, applicable chiefly to laboratory trials and crop cultivation in greenhouses, owing to the fact that the treatment was applied to seedlings, which could not be handled on a bulk basis like seeds.

TOLMAČEV (1929) came even nearer to the development of a technique which could be used in agronomic practice. His aim was to keep the seeds in the form of seeds for as long a period as possible, and yet at the same time to break their dormancy and permit growth to start very slowly. This was presumably done because it was considered that the temperature during or just after germination is the effective factor in inducing subsequent flowering, and at the same time to provide treated grains, not seedlings, which might still be sown in the normal manner. Working on winter wheat, for example, TOLMAČEV applied partial soaking to retard growth during germination; by keeping such seed for 2 months at O°C., he obtained plants which produced ears in the first year when sown in spring, even after the latest date of sowing. Similar results are claimed with sugar beet, and conversely, it is stated that a sugar beet plant can be maintained in a vegetative condition for at least 4 years by withholding that factor of the environment (temperature) appropriate for development.

To explain these results, practically identical with the results of vernalization described below, TOLMAČEV produced what MAXIMOV has described as a "peculiar theoretical interpretation." According to TOLMAČEV, winter cereals will not ear nor will sugar beet flower until a definite active phase has been completed in their "stem plasm," a definite work must be done and a sufficient amount of the products of disintegration accumulated. In spring plants, the stem plasm is ready for its function at the time of seed maturity. Those conditions, for instance, low temperature, which stimulate the accumulation and preservation of the products of distintegration, also stimulate fruit bearing, and on the contrary the absence of the accumulation of the products of disintegration during intensive growth under the influence of light and high temperatures depresses stalk formation.

U.S.S.R.: — Working at the Experiment Station at Ganja in Azerbaidžan, LYSENKO observed the influence of the thermal factor on the duration of the developmental phases in cereals and cotton (1928). It was

Н. К. З. А. С. С. Р.

آ س. ش. ج. خلق توپراق قوميسارلغی

Труды Азербайджанской Центральной Опытно-Селекционной Станции

им. тов. Орджоникидзе в Гандже.

Выпуск 3.

Т. Д. ЛЫСЕНКО.

Влияние термического фактора на продолжительность фаз развития растений.

ОПЫТ СО ЗЛАКАМИ И ХЛОПЧАТНИКОМ

Baku — 1928.

Title page of Lysenko's first article on "Effect of the Thermal Factor on Length of Phases in Development of Plants," published in the Trudy of the Azerbaidžan Experiment Station, No. 3 (1928), *cf.* p. 38.

found that the time required for the completion of some of the recognizable stages in the growth of cereals such as seedling emergence, ear emergence, full flowering, wax ripeness, etc., are completed more rapidly at higher temperatures than at lower. It was noted, however, that in spring and more especially in winter forms the phase of shooting (ear formation and elongation of internodes) does not always show this relation. With an increase in the temperature at which the crops are grown, this phase is in some cases initiated earlier, and in others takes place later or not at all. When absent, the plants remain at the tillering or rosette stage. LYSENKO called this retention of the winter habit "hibernalism," that is, the property of plants to remain for an indefinitely long period at the phase of tillering without flowering stems.

After moving from Azerbaidžan to the Institute of Plant Breeding and Genetics, Odessa, LYSENKO continued to study, in collaboration with DOLGUŠIN, this property of hibernalism in cereals and the nature of the difference between spring and winter forms. The results of the experiments carried out for this purpose were presented at the All-Union Congress of Genetics, Selection, Seed Production and Animal Production in 1929 (DOLGUŠIN and LYSENKO, 1929), and may be indicated from the following quotation of their conclusions:

(*a*) Experiments on time of sowing showed that there are no definite dates which can be used to distinguish winter forms from spring forms. The later the date of sowing, the larger is the number of varieties which retain the winter habit; when varieties are sown in the second half of April, or even later under the conditions of Azerbaidžan, not only all the winter and alternative forms but also the majority of the spring forms remained at the tillering stage.

(*b*) One of the main factors preventing shooting is the high temperature of the period subsequent to sowing. However, after a pre-sowing chilling of slightly sprouted or imbibed grain at 2.5 to 3.5° C. for a definite period varying according to variety (Kooperatorka wheat = 38 days; winter barley = 28 days), winter cereals will proceed to the shooting stage no matter when sown. After such a pre-sowing treatment, the rate of shooting increases according as the temperature of the period following sowing itself increases. Since a high temperature after sowing retards shooting in plants raised from unchilled grains, it is argued that in cereals the period from seed swelling to ear emergence covers at least two biologically consecutive phases. The first of these does not produce any morphological changes in the plant and is directly related to the thermal factor, high temperatures prolonging its duration. (Compare with the condition of ripeness-to-flower postulated by KLEBS, 1918). The duration of the second phase (shooting) is, like all other phases, inversely related to temperature, progressing most rapidly at the higher temperatures.

(*c*) Thus, the retardation of shooting observed in cereals sown without pre-treatment and subjected to a high temperature after sowing is due to the prolongation of the unrecognizable phase; if the temperature of the period after sowing reaches a maximum at and beyond which this phase for a given variety cannot be passed, then this variety will behave as a winter form, and will not ear.

(*d*) Since the temperature of the environment rises with the approach of summer, it is observed in sowings of a mixture of varieties that the later the sowing, the greater is the number of varieties which change from a spring to a winter habit.

Having worked out a thermal constant for a number of varieties, LYSENKO and his associates at Odessa proceeded to apply this particular method of chilling to slightly sprouted grain of cereals and seeds of other crops. In 1931 and 1932, LYSENKO published instructions for the treatment of seed by this method (jarovizacija) which came to be known in countries other

than the Soviet Union as vernalization (Imperial Agricultural Bureaux, 1933). The technique had as its theoretical basis the principle of phasic development. Although it is not possible to discuss this controversial hypothesis here, it is necessary to give the principles postulated by LYSENKO in order to appreciate the Russian interpretation of the results obtained in this work.

In the 4 or 5 years up to and including 1934, LYSENKO formulated his theoretical conceptions as follows:

(*a*) growth and development are not identical phenomena;
(*b*) the entire process of the development of an annual seed plant consists of individual *étapes* or stages;
(*c*) the stages or phases always occur in a strict sequence, and a subsequent stage cannot commence until the preceding stage has been completed;
(*d*) different stages of development of the same plant or crop require different environmental conditions for their completion.

These postulates are related to the technique of vernalization in the following way. If growth and development are not identical phenomena, it should be possible to reduce the rate of progress of growth to a minimum while allowing for rapid development. LYSENKO expressly confines his distinction in terms of the *rate* of growth and development, the former meaning the rate of accumulation of dry matter or increase in size of a plant, the latter meaning the rate of progress through the stages of development as postulated by him. The technique of vernalization is based on a very reduced rate of growth, in order to prevent formation of seedlings, combined with a rapid rate of development under the influence of the optimal environment, that is, low temperature.

Discussion of postulates (*b*) (*c*) and (*d*) is outside the scope of this review, but it should be noted that LYSENKO assumed that the low temperature used in the vernalization technique is an obligatory requirement for a certain phase of development; once that requirement has been met, the seed, seedling or plant can proceed to the next phase. This strict sequence of phases is strongly criticized by physiologists in other countries; a number have expressed the view that low temperature is not obligatory for ultimate reproduction, and that vernalization by short day is possible. If it is supposed to be the light period of a short day which has the vernalizing effect, obviously this could not operate on soaked grain kept in complete darkness.

According to the Russian literature, vernalization rapidly became a regular agronomic practice throughout Russia. It was used to ensure reliable crops in regions in which the growing period was short owing to frost or drought, or to ensure the production of two crops per season on the same land (for example, a grain crop followed by a catch crop for green manure or forage). Courses for farmers were held at the Institute at Odessa and elsewhere. In most parts of Russia the low winter temperatures made it possible for farmers to vernalize their grains and seeds in the barns, once the elements of the technique had been acquired.

From data collected by M. A. OLJHOVIKOV, the following acreages in the U.S.S.R. were sown with vernalized seeds in the years 1932-7 inclusive:

1932	43,000
1933	200,000

1934	600,000
1935	2,100,000
1936	7,000,000
1937	10,000,000

More recent data have not been seen; it is not known to what extent, if at all, Russian farmers are now using the method, or whether any centres for treatment and distribution of vernalized seeds have been operating.

From an academic point of view, the technique of vernalization, and more particularly the theoretical principles which were evolved on the basis thereof, received a great deal of attention among Russian physiologists. Writing at the request of the author, MAXIMOV (1934) stated that the doubts and contradictions that had arisen would suffice to show that the theory was far from being completely formulated. "A single investigator or group of investigators around him are, of course, unable to solve all the most difficult problems of the physiology of development," problems which now open to physiologists and others an extensive and fertile field of research.

One of the early interests of Russian investigators in connexion with vernalization was in the possibility of diagnosing whether seeds had had their total treatment required. Methods based upon a staining technique or on the change in iso-electric point were tried, but no satisfactory conclusion seems to have been reached. Other investigators wrote on subjects such as the relation of enzymes and hormones to vernalization, the physiological and biochemical characteristics of vernalized as compared with untreated seeds, and of the plants produced from these seeds. The outlook on the breeding of crop plants changed, the emphasis then being placed on the need for preliminary analyses of environmental requirements followed by breeding based upon these specific and varietal characteristics. All these aspects are discussed more fully elsewhere (WHYTE, 1946); it is at present desirable to refer to two particular aspects of this work in the U.S.S.R., namely, the hormonal interpretation of development with particular reference to the vernalized grain (CHOLODNY, 1939, see also ČAĬLAHJAN, 1937), and TUMANOV'S work on the relation between developmental phases and winterhardiness (1940).

A considerable amount of literature has accumulated on the evidence for and against the existence of a hormone which causes flowering in plants. It appears that some such substance does operate, but it has not yet been possible to isolate it, still less to apply it to plants by injection or other methods in order to induce flowering. This hormone is, however, generally associated with the action of light upon leaves, and is assumed to be responsible for transmitting a response taken up by a leaf to the growing point under its control, causing it to exhibit the characteristics either of growth or development. CHOLODNY has, however, produced an interpretation of the low temperature effect associated with vernalization based on the existence and operation of a hormone.

The investigations of SCHANDER (1934), CHOLODNY (1935), LAIBACH and MEYER (1935) and others have shown that seeds contain reserves of various hormones received from the mother plant and concentrated chiefly in the endosperm or cotyledons. This reserve is believed to come into

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action during germination, in the early stages of which the phytohormones are transmitted to the organs of the embryo which are beginning their growth and development. SCHANDER showed that the activating substances contained in cereal grains at the very beginning of germination pass over to the embryo through the special elongated cells of the aleurone layer, and regarded these substances as being required for further development and growth of the embryo. CHOLODNY (1935) claimed that auxin or a related compound which is accumulated in the endosperm during germination of cereal grains is also transmitted into the embryo. This auxin has been identified as indole-3-acetic acid (HAAGEN-SMIT, LEECH and BERGREN, 1942); it is rapidly liberated from its storage form in the endosperm by simple moistening or alkali hydrolysis, differing in this respect from the auxin in leaves and stems (THIMANN and SKOOG, 1940).

In 1936 CHOLODNY formulated the nature of the internal factors which act upon the growing points during vernalization. According to the hypothesis which he developed, the embryo is stimulated to activity by the pre-treatment technique but lacks the capacity for normal growth, because of the insufficient moisture and low temperature accompanying the vernalization treatment; the embryo absorbs from the endosperm the growth hormones which are stored there in great quantity. As these hormones are generally used primarily for growth, and as under the conditions of the vernalization treatment there is almost no growth, the concentration of the hormone in the cells of the embryo is assumed to have risen considerably above the normal for that stage of the plant's life. It is further assumed that this increase of the intracellular concentration of the hormone in the growing points causes an acceleration in the progress of the meristematic cells of the young plants through the first phases of development. Thus the interval of time which separates these first phases of development from the later stages associated with preparation for fruiting is shortened. The full result is assumed to be that the whole cycle of plant development is completed sooner than it would be under normal conditions (CHOLODNY, 1939).

Reference will be made in a later section to the experiments of GREGORY and PURVIS on the vernalization of excised embryos, on which they base their own criticism of CHOLODNY's hypothesis. CHOLODNY felt the need to introduce a correction into his hypothesis because of the rapid advances being made in the knowledge of phytohormones. "It is hardly possible at the present time to doubt that the *qualitative aspect* of the complex of phytohormones acting upon the embryo is not also without its own effect upon the development of the embryo. The composition of that complex and the chemical nature of the active substances found in the tissues of the embryo and of the plant developing from it undoubtedly also change under the influence of the external and internal conditions in which development is being maintained."

CHOLODNY considers that his working hypothesis is confirmed by some of his own experiments on the pre-treatment of seed with various solutions of indole-acetic acid, and blastanin or embryo extract (CHOLODNY, 1936), as well as by some later experiments by THIMANN and LANE (1938) and by ČAĬLAHJAN and ŽDANOVA (1938). These investigators found that a short treatment of growing seeds with increased concentrations of phy-

tohormones affected the subsequent development of plants, what might be called "vernalization by hormone." In some cases it was claimed that the growth of the vegetative organs was either inhibited or accelerated; in others fructification was intensified and occasionally a conspicuous curtailment of the vegetative period was recorded. The whole question has however been experimentally investigated by HATCHER (1943) and HATCHER and GREGORY (1941) whose work is reviewed later.

This work has completely negated the theory of CHOLODNY. As far as the hormonal treatment of seeds is concerned, the balance of evidence is at the moment against any after-effect of the above nature (TEMPLEMAN, 1939; STEWART and HAMNER, 1942), although HAMNER (1938) has referred to a U. S. Patent being taken out by one WENDT for the application of acetylene to pineapple plants. HAMNER states: "The prompt differentiation of flower primordia and fruit development which ensue in treated plants as compared with non-treated plants which differentiate flower primordia many weeks and even months later is worthy of critical experimentation."

In his book entitled "The physiological bases of winterhardiness in cultivated plants," TUMANOV (1940) deals with the literature on a number of aspects directly or indirectly related to developmental physiology, including the relation between winterhardiness and phasic development as understood in Russia. In the research of VASILJEV (1934), KUPERMAN (1936), KUPERMAN and ZADONČEV (1936), SALTYKOVSKIĬ and SAPRYGINA (1935) and others, it has been claimed that frost resistance is connected with phasic development. These experiments were made chiefly with winter cereals; frost resistance was found to be generally lower, and at times conspicuously so, in plants from vernalized seeds, that is, from seeds with embryos which had, as far as could be ascertained, completed the thermo-phase, to use the terminology of phasic development. The following percentage survival of wheat plants observed by TUMANOV (1935) is quoted as an example:

	VERNALIZED	UNVERNALIZED
Ukrainka: early sowing	16	92
Ukrainka: late sowing	12	94
Moskov. 02411: early sowing	7	93
Moskov. 02411: late sowing	0	96

TUMANOV and IVANOVA found that both early and late sowings of vernalized grain of Lutescens wheat became depleted at higher temperatures (−11 to −12°C.) than sowings from unvernalized grain, and that generally the frost resistance was higher with the shorter periods of presowing vernalization. After 20 days of vernalization of winter wheat and 15 days in winter rye, the frost resistance of the resulting plants was conspicuously reduced.

Special investigations conducted in the Leningrad region indicate the risks to which autumn sowings were exposed when the early autumn temperatures favour the natural vernalization of seeds after sowing. When Lutescens 0329, Moskov 02411 and Minhardy had been sown at the end of August, they were found to have completed their thermo-phase on Jan. 13

in 1934-5, on Jan. 1 in 1935-6, and almost entirely by Nov. 19 in the 1936-7 season.

Such a variation in time of completion of the thermo-phase cannot be attributed to variation in climatic conditions alone. A partial or complete vernalization as far as the thermo-phase may occur while the developing grain are still attached to the mother plant, and is also regarded as possible during prolonged drying on the field in a cold and wet season, when the seeds may be sufficiently imbibed to begin the slow growth necessary before development through the thermo-phase can begin.

TUMANOV recognizes two possibilities resulting from the after-sowing vernalization in the open: (*1*) the seeds may be completely vernalized before the beginning of winter, (*2*) the vernalization of the thermo-phase may be completed either by the beginning of winter or during the winter. In the first case, especially when the plants have had an opportunity to grow for a considerable period, they would lose their ability to harden, and their resistance to frost would thus be much reduced. Some investigators believe, however, that frost resistance begins to fall in vernalized plants with the beginning of the photo-phase. Some investigations have indeed shown that the capacity to resist frost falls rapidly when the plants are grown after completion of the thermo-phase under conditions which favour the progress of the photo-phase, namely, high temperatures and long day. On the other hand, TUMANOV states that a fall in frost resistance may also be noted when plants are grown under conditions not favouring the photo-phase, as may be the case with late autumn sowings of vernalized seeds.

TUMANOV refers to his own investigations in 1936/7. When the plants were tested on Nov. 2, and the thermo-phase was not completed until Nov. 19, frost resistance was found to be reasonably high; the percentage of survival in Lutescens 0329 at –12 to –18°C. varied from 98 to 84. When the plants were tested on Dec. 14, that is, 25 days after the end of the thermo-phase, frost resistance had fallen, percentage survival varying from 85 to 27 at temperatures of –13 to –22°C. Before the tests were made, all plants had been kept under conditions which would ensure their hardening. In these investigations, the loss of the capacity to resist frost was observed only when plants were grown for some time after the completion of the thermo-phase; this was the case with winter rye, Vjatka, the percentage survival being 78 to 44 in the first test, and only 25 at –13°C. in the second test, while no plant survived temperatures lower than –15°C.

The situation is different when the thermo-phase is completed so late that no growth is possible before the plants are frozen. In TUMANOV's investigations in 1935/6, when vernalization was completed by Jan. 1 in winter wheats and by Dec. 1 in winter rye, the percentage survival at –14 to –18°C. varied from 96 to 74 in Lutescens and from 81 to 70 in Vjatka. Similar results were obtained in another experiment where the percentage survival was much higher after later sowings.

It may be noted at this point that OLEĬNIKOVA has shown that the thermo-phase can be completed in the open during the winter under the snow cover in the winter conditions at Leningrad. Winter wheats were sown on Nov. 17, Jan. 1, Feb. 1, and March 1 and 31 in the open; from the beginning of April, the various series were transferred to greenhouses

where the temperatures were such as to prevent any further progress through the thermo-phase by those plants which had failed to complete this phase in the open. Winter rye failed to ear only after the last date of sowing, and winter wheats after the last two dates. It is therefore concluded that, even in strongly "winter" plants, the thermo-phase may be fully or partially passed during the winter.

TUMANOV considers that the completion of the thermo-phase alone does not yet necessarily mean that frost resistance is markedly reduced, provided the conditions for subsequent growth are not present. Different conditions arise, however, under a deep snow cover or during a temporary thaw, when plants may resume active growth very readily and would thus have a reduced resistance to frost. TUMANOV considers it possible that, after the thermo-phase, the growing point is capable during resumption of growth of changing the state of the protoplasm in all other tissues in existence at that time, and suggests a hormonal mechanism as the possible explanation.

KUPERMAN (1936) produced evidence that vernalized plants accumulated much smaller quantities of sugars than unvernalized plants, but TUMANOV and FEDEROVA found that vernalized plants have sufficient amounts of sugars and that a sugar deficiency cannot be regarded as the reason for their lower frost resistance. The amount of sugars in vernalized plants first rose very slowly and later, in April, more or less rapidly, reaching 26 per cent on May 7, or 10 per cent lower than in unvernalized plants, and similar to unvernalized plants before wintering.

TUMANOV and IVANOVA found that the exposure of vernalized plants to the conditions requisite for the second phase of hardening had no effect, although it is during this phase (of hardening) that plants should show a considerable increase in their frost resistance. TUMANOV therefore assumes that those changes that originate during vernalization cause the protoplasm to be readjusted in such a way that it loses the ability to undergo the appropriate changes during the second phase of hardening, regardless of the presence of protective substances, dehydration and low temperatures.

Since enzymatic processes are very active during the period of germination, it was natural that studies should be made of their behaviour in relation to vernalization. Whether any change which may be noted in their activity is governed ultimately by the concentration of hormones present depends upon the confirmation of CHOLODNY's hormonal interpretation of vernalization. The studies on enzymes in relation to vernalization made by RICHTER and his associates and DEMKOVSKIĬ, and on the iso-electric point by RICHTER, GAVRILOVA and others, are described in the early reviews of vernalization (I.A.B. 1935).

OVEČKIN and others (1936) studied the biochemical changes in winter wheat grains during vernalization. Grains were vernalized at 0 to 1°C. under normal air conditions, and also in a 0.003 per cent concentration of chloroform or ethylene chloride. Samples were taken on every sixth day and records made of respiration rate, sugar content, catalase activity, content of mono-amino-acids and reduced glutathione, and of the percentage of fully vernalized grains that grew when planted out of doors. The presence of chloroform and ethylene chloride reduced the percentage of fully vernalized grains; the respiration rate, catalase activity, and content of reduced

glutathione were all lower in grains vernalized in ethylene chloride. The oxidation-reduction processes are intensified during vernalization, but there is no relation between content of sugars and mono-amino-acids and vernalization.

Sapožnikova (1935) analysed vernalized seed of *Lupinus angustifolius*. The content of reducing sugars in seeds treated at 6 to 7°C. increases with the progress of vernalization, a fact regarded as suggesting an increasing activity of the enzymes acting on carbohydrates; however the content of reducing sugars gradually falls in seeds vernalized at 4 to 5°C. The amount of active enzymes rises with vernalization at 6 to 7°C. to a maximum on the last day of treatment; enzymes increase less rapidly with vernalization at 4 to 5°C. during the first 12 days and then fall. The control of active enzymes is measured by their activity at 35°C. The protease content in seeds vernalized at 6 to 7°C. was found to rise to a climax on the day of sowing, while in those vernalized at 4 to 5°C. its changes were indefinite. The activity of catalases, peroxidases and respiration varied in the different series. Marked activity of catalases and peroxidases is a feature of vernalized lupine seeds that give rise to plants with a reduced vegetative period, and this character is stated to be useful for distinguishing vernalized from unvernalized seeds.

From determinations of nitrogenous substances (total N, insoluble and soluble N, amino-N, amide-N, and ammoniacal N) in seeds and plants during vernalization and in those under conditions which prevent vernalization, Konovalov (1938) found their behaviour to vary considerably. When vernalization was prevented, the disintegration of the proteins extended to the end products, whereas during vernalization the proteins retained their form, but became more readily soluble. This worker concludes that nitrogenous substances appear to be re-synthesized during vernalization, and regards this transformation as a distinctive feature of the vernalization process. Paševič (1940) found that vernalization induces changes in the protein substances of the wheat germ affecting both their colloidal state and their amino-acid content.

In some early studies on the effect of vernalization on the rate of accumulation of dry matter, Konovalov (1936) found that vernalized plants of wheat and lentils accumulated more dry matter per unit of time than the unvernalized control, and the yield of organic matter was consequently increased. More recently, Konovalov and Popova (1941) found that the synthesizing capacity of vernalized plants is higher than in the unvernalized controls. By the time of earing, vernalized plants contained 26 per cent more organic matter than those from soaked and germinated seeds and 52 per cent more than plants from seeds sown dry.

Konovalov (1944) has continued his work at the Timirjazev Institute of Plant Physiology, Moscow, on the effects which vernalization of seed exerts on the growth and physiological processes in the leaf relative to the yield of grain or seed ultimately produced. The chief concern in these experiments has been productiveness of a plant as governed by the intensity of photosynthesis, the extent of its leaf area, and the duration of activity by the leaves.

The intensity of photosynthesis was not materially affected by vernaliza-

tion, but the interval between emergence of the leaf and its death was shortened. The factor most closely connected with yield was leaf area of a plant, and it was this which was markedly affected by vernalization. The successive emergence of leaves was more rapid with than without vernalization, and each leaf reached its maximal size sooner. A growing leaf uses much of the products of metabolism for its growth; vernalization has the advantage of hastening the growth of leaves and ensuring its early completion, after which the products are released for the benefit of the embryonic ear. It was noticed that the content of nitrogenous substances in the lowest leaves was diminished after the leaves had ceased to increase in size.

The synthetic activity of the leaves reached the maximum sooner in vernalized than unvernalized plants, and, after remaining stationary for a while, gradually decreased. The accumulation of dry-matter was likewise more abundant in vernalized plants. Consequently there was more material available for translocation to the developing ear, thus accounting for the well-being of vernalized plants which is to be especially observed during a dry season.

The yield of late-maturing wheat in KONOVALOV'S experiments was increased by vernalization because, although tillers were reduced in number, their ears bore better and more numerous spikelets, as well as more numerous and heavier grain. In the early-maturing varieties the good development of the ears could not compensate for the reduced number of tillers, and vernalization did not therefore increase the yield.

A similar result is reported by BUZOVIR (1936), who made experiments over two seasons with varieties of winter and spring wheat and a variety of millet; at the beginning of vegetative growth in winter wheat and throughout the vegetative period in the other plants, the rate of elaboration and accumulation of dry matter was greater in vernalized plants. The accumulation of carbohydrates was also greater in vernalized plants, particularly during the period from jointing and stem elongation to milk ripeness.

In experiments made by ZAĬCEVA (1939) with spring and winter wheats sown with vernalized and unvernalized seeds, it was found that the chlorophyll content increased as the plants advanced towards sexual maturity, reaching a maximum of over 6 mg. of crystalline chlorophyll per grm. of leaf weight in both varieties, by the time of heading or thereabouts and falling rapidly thereafter. In rapidity of development, the spring wheat was somewhat ahead of the vernalized winter wheat. No such regularity was noted in unvernalized winter wheat plants that remained at the tillering phase, the chlorophyll content varying from the beginning of tillering between 3 and 4 mg. of crystalline chlorophyll per grm. of leaf weight, the highest figures being obtained in the leaves nearest to the spikes. Advance in development is considered to be the chief factor causing this conspicuous variation.

An important aspect of Soviet research is the work of KOSTJUČENKO and ZARUBAĬLO on the vernalization of grain during the period preceding dormancy while the grain is ripening on the mother plant. This is a question which has very considerable practical implications, and affects all matters connected with plant introduction and the cultivation of plants in an environment differing widely from that in which the seeds were produced.

The experiments of KOSTJUČENKO and ZARUBAĬLO are discussed along with those of GREGORY and PURVIS on the same aspect in a later section of this review.

Another small point may be mentioned before leaving the Russian research on vernalization. It has been found that not all plants can be vernalized in the form of seeds or grains, and that the low temperature applied does not begin to have an effect on certain types until a seedling has been formed. This applies more particularly to certain species of *Brassica* such as rape and turnip.

Germany: — The name of Professor W. RUDORF of the Kaiser Wilhelm-Inst. f. Züchtungsforschung, Müncheberg, Mark, is chiefly associated with work on and reviews of vernalization as applied to German conditions and crops. A review of the literature on vernalization was published in 1936 (RUDORF and HARTISCH, 1936), and a summary of experiments made at Müncheberg, Giessen, Göttingen, Berlin, Berlin-Dahlem, Heidelberg and Leipzig was published in 1938 (RUDORF, 1938*a*). RUDORF himself studied the relation between vernalization and photoperiods and resistance to cold.

Using winter, dual-purpose and summer forms of wheat and barley, RUDORF (1938*b*) applied different temperatures and different photoperiodic treatments with a view to discovering a method of producing material for studying the physiological causes of cold resistance. Resistance to cold under periods of chilling ranging from 20 to 60 days at 3 to 5°C. was determined, and it was found that such resistance is largely governed by the condition of the plants in the dormant period before the thermo-phase has been completed, that is, before vernalization is complete. The more this internal condition is degraded by vernalization the less is the resistance to cold. Varietal differences are noted; in certain varieties a reversal in the reaction can be seen after 60 days' chilling. It remains a question whether such a turning point can also be determined in definite winter forms chilled for more than 60 days. When the thermo-phase has been partially completed, the capacity to harden is annulled to a degree which is in proportion to the duration of the treatment. The further work which was then stated to be in progress was the discovery of varieties with as long a thermo-phase as possible (maximum requirement of low temperature) and the maximum cold resistance at that phase, and the discovery of varieties which would still exhibit great hardening capacity even after completing the thermo-phase.

In 1936 HARDER and STÖRMER (1936) showed that white mustard (*Sinapis alba*) responded to temperature of germination best in short-day conditions. An exhaustive comparative study of vernalized mustard and oats made by VON DENFFER (1939) under a series of daylengths artificially maintained showed that this different behaviour of these two plant types occurred in the time between initiation of flower primordia and flowering. The relative shortening of the purely vegetative phase from germination to the visual appearance of flower buds in mustard, and shooting in oats, was on the other hand approximately the same for all daylengths (from continuous light down to 12 hour day) as compared with control plants which had not been vernalized.

The increase in duration of vernalization led in both mustard and oats

to a gradual shortening of the vegetative phase, which asymptotically approached a limiting value. This occurred in winter oats (var. Eckendorfer) after 80 days treatment, in mustard after 50 days vernalization. The limiting duration of the vegetative phase after optimal duration of vernalization was dependent upon the daylength under which the plant was grown; being minimal in continuous light, maximal in short days. The extension of daylength leads in both plant types to a gradual shortening of the vegetative phase, and again approaches a limit value. The limiting duration of the vegetative phase under optimal photoperiod is dependent upon the duration of vernalization.

The leaf number on the main shoot of oats is directly related to the development, as McKinney and Sando showed for wheat, and Purvis and Gregory for Petkus winter rye; the same direct relation between leaf number and time of flower formation was established also in *Sinapis alba*. The results can be interpreted without difficulty along the lines of the flower hormone hypothesis of Purvis and Gregory.

Rudorf, Stelzner and Hartisch (1937) described a technique for vernalizing seed at high temperatures, presumably for use with crops such as soybeans. The aim in this work was to prevent fungal and bacterial growth and to avoid excessive elongation of the seedling. It is necessary to keep the seed in motion and at the same time to maintain the temperature and moisture in the seed containers within the desired limits; a certain amount of aeration must be practicable and it must be possible to darken the whole apparatus. A portable apparatus is described, movement being secured by the use of small disinfection drums.

Germany is a borderline environment as far as the cultivation of soybeans is concerned, yet the wide range of products that can be obtained from this crop made it desirable to grow it wherever possible. Experiments have therefore been made on the manipulation of development of this crop. Rosenbaum (1937*a*, 1937*b*) attempted to vernalize soybeans; although agreeing that the conditions of treatment laid down by Lysenko are practically correct, it is considered that similar effects may be attained with other temperatures, and that, by suitable adjustment of the conditions of growth and development, the vernalization treatment may be dispensed with entirely. The environmental conditions following sowing are stated to govern the course and rate of development more than does previous vernalization, for which reason it is considered to be difficult to make reliable comparisons of the results of vernalizing different varieties. A reduction in time taken to flower may be more readily obtained by means of the photoperiodic aftereffect, although this is said to entail a reduction in yield. Rosenbaum does not recommend either vernalization or photoperiodic induction of soybeans for the use of the practical farmer or the plant breeder in Germany.

Another German worker who does not consider that a thermo-phase is obligatory in winter wheat is Voss (1938). By using short day under conditions of a constant high temperature of about 20°C., it was found possible to induce shooting in German winter wheats. The manner in which a variety reacts to treatment may differ within the variety under (*a*) combined cold and short-day treatment, and (*b*) short-day treatment alone, at high temperatures. Given a very long growth period, winter wheat

may be brought to flowering even under continuous illumination and high temperatures. Having found that winter wheat can pass from the vegetative to the reproductive state most readily under the influence of different external factors, in particular low temperature and short day operating alone or in combination, Voss suggests a new definition for "winter wheat" and "summer wheat." Wheat varieties which, under a constant high temperature (approximately 20°C.), constant illumination (by natural or artificial light not exceeding 1500 lux), and otherwise favourable conditions in a greenhouse, do not begin to shoot within 4 to 6 weeks are described as winter wheats.

Great Britain: — The chief work on the vernalization of cereals in England began about 1931 at the Research Institute of Plant Physiology, Imperial College of Science and Technology, London and 1934-35 at the School of Agriculture, Cambridge. BELL (1935, 1936) worked at Cambridge with wheat, barley and oats, but the experiments were not continued and BELL has since investigated the developmental physiology of sugar beet (see BELL and BAUER, 1942, and WHYTE, 1946). In his work on cereals, an acceleration in earing was observed in the winter varieties of barley and wheat but none in the oat varieties. Many of the varieties giving the greatest response in the early stages (more rapid germination) showed no acceleration in earing, and conversely the winter varieties in which vernalization produced the maximum difference in earing date showed little or no early response. The type of response is a varietal character.

Following upon these experiments, a series of sowings was made with vernalized and untreated seed of winter and spring varieties of barley, wheat and oats, one in October and six successive ones in the following spring between Mar. 8 and April 5. The treatment consisted of exposure to 3°C. for 14 days. All but one of the varieties showed a slight acceleration in germination. The acceleration in earing was slight or nil in the autumn sowings, but in the spring sowings there was a progressive increase in acceleration with delay in sowing in the winter varieties and, conversely, a progressive decrease in the spring varieties. This difference in behaviour is attributed to the rise in temperature with progressive lateness of sowing; greenhouse sowings under higher temperature came into ear sooner than field sowings in spring varieties and later in most winter varieties, showing that low temperatures in the open had effected a certain amount of vernalization. Examination of growing points was also made in these trials and revealed great differences in varietal behaviour.

The long series of experiments made by GREGORY, PURVIS and other workers of the Research Institute of Plant Physiology, Imperial College of Science and Technology, South Kensington, has provided valuable data on the fundamental biological processes concerned in the response of growing seed to vernalization. The work on effects of temperature during germination was embodied in a publication (PURVIS 1934) on the analysis of the influence of temperature during germination on the subsequent development of certain winter cereals and its relation to the effect of length of day.

Winter rye (var. Petkus) was the experimental material used. One series was grown in normal long day at high and low levels of nitrogen sup-

ply and subjected to temperatures of 1°C. and 18°C. respectively during germination; a second series was grown in short day of 10 hours with similar temperature treatments. In the long-day series, cold germination reduced the time required for earing and flowering, not so in the short-day series. Low temperature in the long-day treatment also reduced the rate of tillering, not in the short-day plants. The effects of temperature were found to be independent of nitrogen manuring.

Under long days and after germination at 1°C., flowering occurred 10 weeks after planting out; after germination at 18°C. it was delayed until autumn when a few ears appeared. Under short days ear emergence was indefinitely delayed after both temperature treatments. Examination of the growing points revealed, however, that under both temperature treatments and daylengths ear initials are laid down. *After germination at* 18°C. flower initials are laid down *earlier in short days than in long days* and the number of initials is considerably increased, and with it the potential grain-yielding capacity. Such ears, however, die within the leaf sheaths, and the stems fail to elongate. After germination at 1°C. the characteristic temperature after-effect, namely, early flower differentiation, was manifest only under long days while under short days the effect was slight. When plants which had received some weeks of short-day treatment were subjected to long days, ears were rapidly formed after germination at 1°C. and more slowly after germination at 18°C. Even with plants germinated at high temperature, flower differentiation may be induced by short-day treatment alone, showing that cold germination is not essential for reproduction. Stem elongation and ear emergence, however, fail unless long days are given subsequent to ear differentiation. These results illustrate a point stressed from the start in the work from this Institute, namely, the great importance of determining the time of formation of the flower primordia rather than the time of emergence of the inflorescence in studies of this kind.

The concept of minimal leaf number has also been a characteristic of the work of Gregory and Purvis. Observations made by Purvis (1934) on the spike primordia indicate that a minimal number of leaves must be formed before the differentiation of flower initials can occur. Under short-day conditions this is always about twenty-two, irrespective of variety and temperature, while under long-day conditions the minimal number is less for plants germinated at low than at high temperatures, namely, 12 for the former (in this particular experiment) and 22 to 25 for the latter. This reduction in leaf number combined with the more rapid elongation of the spike leads to acceleration in the onset of floral differentiation and thus induces a behaviour more closely resembling that of spring varieties in which the minimal number is only seven. The effect of the greater minimal number of leaves required before "ripeness to flower" is attained in short days is partially counterbalanced by the higher rate of differentiation of the ear in these plants, particularly in those germinated at low temperatures. The increased rate of floral differentiation in short days also affords an explanation of the photoperiodic after-effect observed by Rasumov in short-day plants like millet. However, in long-day plants like oats or barley, the floral differentiation is almost independent of daylength, only the later stages being

hastened by long day. All spring cereals are also of this type. On the other hand, winter rye behaves as a long-day plant only when germinated at low temperatures. When germinated at 18°C. the floral differentiation shows the typical short-day behaviour, being promoted by short day, though stem elongation and further stages of floral development still retain the long-day reaction. Thus the effect of chilling in winter cereals sown in the spring is to reduce the minimal number of leaves required for flower initiation and to enable the plant to attain the condition of "ripeness to flower" at an earlier date while long days still prevail. It is in this way that PURVIS interprets the phenomena connected with vernalization.

After a review of vernalization as a method of hastening flowering (PURVIS, 1936), PURVIS and GREGORY proceeded to a comparative study of vernalization of winter rye by low temperature and short days, the first of a series of papers published (1937) under the general title of "Studies in Vernalization of Cereals," aiming at a closer analysis of the proximal cause of the effect of the low temperature applied during germination. A preliminary report appeared in *Nature* (GREGORY and PURVIS, 1936*a*).

The treatments with low temperature or preliminary short days both resulted in acceleration of flowering. With the low temperature treatment, 4 days' exposure produces a definite response; the magnitude of the response increases with the duration of treatment up to a limit of 14 weeks, after which the flowering behaviour of winter rye is indistinguishable from that of spring rye. With increasing exposure to low temperature the leaf number in winter rye is reduced from approximately twenty-five to seven.

With the exposure of seedlings of winter rye to preliminary short days (10 hours) the magnitude of the effect on flowering increases with length of treatment up to 6 weeks, but longer exposures retard flowering. Reduction of leaf number to a minimum of sixteen occurs after 6 weeks' treatment with short days, but longer treatment again leads to increase.

In both spring and winter rye, PURVIS and GREGORY state that there is a minimal leaf number, seven, which cannot be further reduced, and a maximum, about twenty-five, which cannot be further increased. The primordia between the eighth and twenty-fifth are indeterminate and can produce either leaf or spikelet; each primordium is double, consisting of a flowering branch (spikelet) with a subtending bract, either part of which may be inhibited according to the length of day or temperature of germination.

To explain the mechanism of these reactions of a germinating seed or a seedling to low temperature or short day, PURVIS and GREGORY (1937) postulated the existence of a hypothetical "flower-forming" substance, the effect of which on the labile primordia varies according to the factors to which the plant is exposed. Although stressing that the whole situation is not yet clear, they state that the following facts are established:

(*a*) The hypothetical substance is not preformed in the endosperm and transferred to the embryo, as the embryo isolated from the seed behaves similarly (see experiments on excised embryos described below).

(*b*) The change can be reversed by high temperature (again see below). It appears possible that during vernalization some precursor of a "flower-forming" substance accumulates in the embryo. This substance may be

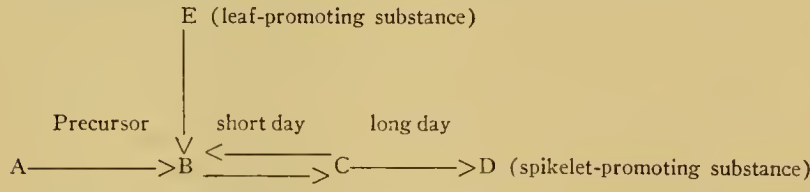
supposed to be translocated and accumulated in all growing points of the shoot, and when a critical concentration is reached induces flower initiation. The increasing rate of formation of primordia indicates that the substance increases autocatalytically. In spring rye about 2 weeks at normal summer temperatures after germination suffice to reach the critical level, while in unvernalized winter rye somewhat less than 6 weeks are required.

(*c*) An oxidative reaction is involved in the formation of the substance, as anaerobic conditions completely inhibit its production during vernalization of winter rye and partially so in spring rye.

During vernalization the "flower-forming" substance or its precursor increases in concentration so that the critical level is reached earlier, and thus spikelet initiation sets in earlier in the sequence of labile primordia, and a progressive reduction in leaf number occurs, finally reaching the minimum of seven characteristic of spring rye. The progressive effect of longer duration of low-temperature vernalization can formally be accounted for on these lines.

The relations to day-length are more difficult to formulate. The outstanding problem here is related to the fact that in both spring and winter rye in continuous short days a maximum leaf number is found, which is approximately constant and independent of temperature of germination. In spring rye the "flower-forming" substance is already present in high concentration, but only in long days do the early members of the series of labile primordia form spikelets. It appears, therefore, that two stages are involved in the process. A precursor depends for its formation on a genetic factor in spring rye and on low temperature of germination in winter rye. This precursor accumulates in all the growing-points, increasing autocatalytically. A second stage in the process involves reactions depending on day-length.

The relations were schematically represented as shown below:



The next experiments reported by Gregory and Purvis (1938*a*) continued the process of narrowing down the problem of the localization of the vernalization effect. It was concluded that the process of vernalization is localized in the embryo itself and is entirely independent of changes in the endosperm or aleurone layer which may take place during germination. It was therefore concluded that the growing embryo is able to synthesize hormones from a simple substratum containing glucose and inorganic salts (including nitrates), and that Cholodny's interpretation based upon the existence of large quantities of blastanin in the endosperm and the increased transference and concentration of this substance in the developing embryo is inadequate.

The phenomenon of reversal of vernalization (devernalization) by high temperature had already been reported by Gregory and Purvis (1936*c*);

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in Studies 2 (Gregory and Purvis, 1938*a*), a loss of vernalization by drying down the vernalized grain for periods longer than 6 weeks is demonstrated by experiment. Although the effect of flowering vanishes, an after-effect is shown by the high tiller production; this is attributed to a reversal in the hormone synthesis noted (as indicated in the diagram above). This line of approach was continued in Studies 3 (Gregory and Purvis, 1938*b*) when anaerobic conditions were utilized to inhibit growth by means other than low temperature. This made possible a successful experimental demonstration of a quantitative reversal of the vernalizing effect of low temperatures by higher temperatures, as well as the complete inhibition of the low temperature effect in the absence of oxygen; and definitely proved that low temperature and not mere inhibition of growth is the essential factor in vernalization.

Continuing the study of the part played by the various tissues of the grain in the process of vernalization, Gregory and De Ropp (1938) found that in the absence of a carbohydrate supply the isolated embryo cannot be vernalized by low temperature. Also it should be noted that previous to the excision of the embryo in the work of Gregory and Purvis the grain had already been soaked in a sterilizing solution for a period of 5 hours. De Ropp (1939) therefore studied more closely the conditions obtaining in the grain during the first few hours of germination, and found that, during the preliminary soaking, a "regulator" controlling its auxin production and distribution enters the embryo from the endosperm and aleurone layer.

The fifth Study in this series from the Research Institute of Plant Physiology concerns an investigation by Purvis (1939) on the inheritance of the spring and winter habit in hybrids between Petkus winter rye and Petkus spring rye. This is thus outside the strict terms of reference of the present review. The cross gave an F_1 generation in which the spring habit was completely dominant, while in the F_2 germination the spring and winter plants were in an approximate 3 : 1 ratio. In the F_2 generation, however, there is within the "spring" and "winter" classes a dispersion of flowering dates, suggesting a less simple inheritance. Purvis explains this on the basis of independent segregation of factors for early and late ripening as distinct from the spring and winter habit. The Russian interpretation of results such as these is discussed elsewhere by Whyte (1946).

Returning again to the question of the nature of the biological processes occurring within a vernalized grain, Nutman (1939) investigated by cytological technique the processes occurring in the embryo-sac of rye subsequent to fertilization; an aspect of direct interest in connexion with the fact that vernalization can be carried out on a developing embryo (see later section of this review). It was hoped to obtain some indication of the functions of the various tissues of the developing fruit and to throw some light on the possible role of hormones in development. This study has led to the discovery of new facts hitherto overlooked, more particularly the part played by the nucellar tissue in the organization of the mature grain and a sequence of degenerative changes associated with each phase of development. Nutman considers the possible role of nekrohormone (or wound hormone) in the development of the rye grain, comparing his observations

with those of La Rue and Avery (1938) on immature excised embryos of *Zizania aquatica* in artificial culture.

Nutman's next investigation (1941) amplified the earlier observation made by Gregory and Purvis (1938*a*) that ears harvested as early as 5 days after pollination produced viable grain, and the earlier observations made on the development of immature barley kernels removed from the plant by Harlan and Pope (1922, 1926). Although the smallest viable grain found by Nutman was only one-sixteenth the weight of normal grain, it was found that all plants whatever their original grain weight reached approximately the same size at the end of their period of growth. Over the greater part of the experiment the plants grown from dwarf grain exceeded those grown from normal grain in (*a*) relative growth rate (on a fresh weight basis), (*b*) rate of tiller production, and (*c*) rate of leaf formation. These three results are attributed by Nutman to a single effect, namely, to the rate of development of the meristem of plants grown from dwarf grains being higher.

Purvis has returned in the eighth paper (1944) in this series to the vernalization of excised embryos. It had already been shown (Gregory and Purvis 1938*b*) that the excised embryo of rye when supplied with nutrient salts and glucose responded to vernalization in the same manner as the whole grain and to a comparable degree. Similar results had previously been reported by Gregory and Purvis (1936 *a*), by Konovalov (1937) and by Bassarskaja and Grossman (1941), and confirm Lysenko's statement that the locus of vernalization lies within the embryo. Further, Purvis (1940) demonstrated "that the isolated stem apex of the embryo, if supplied with sugar and subjected to low temperature, regenerates the whole plant, which shows itself to have been vernalized." McKinney and Sando (1935) noted a similar result when they mutilated embryos before chilling, but maintained the contact with the endosperm. Gregory and De Ropp (1938) had further shown that if sugar is omitted from the medium in which these excised embryos are grown, they remain unvernalized. The general conclusions drawn by these British workers from their experimental results is that the large accumulation of blastanin found by Cholodny (1936) in the endosperm of maize does not play any essential part in the vernalization process; the embryo is capable of synthesizing any hormones that may be necessary for vernalization from external sources of carbohydrate in the presence of inorganic salts, with possibly the aid of additional substances already present in the embryo before imbibition. Embryos excised from *unsoaked* seed can still be vernalized, thus showing that the objection to the excised embryo technique raised by Cholodny (1939) and quoted by Whyte (1939) is not valid.

Purvis enumerates the factors which can possibly participate in the vernalization process as follows:

a) the embryo and its constituents,
b) the source of organic carbon,
c) the source of nitrogen and the mineral salts,
d) the effect of low temperature.

Preliminary experiments conducted in 1939 comprised the subjection of excised embryos to a low temperature for 6 weeks on agar media contain-

ing varying proportions of carbohydrates and nitrogen. A difficulty was experienced in that even on media containing little or no sucrose some degree of vernalization was apparent, and this applied only to a few individual embryos. It appeared that quite small amounts of sucrose were adequate for vernalization and that a source of this sugar may have been available within the individual embryo, either as stored sugars or starch in the tissues or as starch grains adhering to the scutellum. A technique was therefore developed involving periods of starvation for the embryos at high temperature to remove available sugar by respiration and this successfully reduced the variability of the low sugar series, although it raised a further set of problems requiring further investigation. The scope of the eighth study is, however, confined to a consideration of the effect on vernalization of varying the carbohydrate and nitrogen supply, the effectiveness of various carbohydrates in growth and vernalization, and to a discussion of the results obtained "within the limits imposed by the unforeseen difficulties of the experiment."

The whole question of the auxin production in the developing and ripe ear has been systematically studied and its relation to vernalization has been investigated by HATCHER (1945). This work has experimentally tested the hormone hypothesis of CHOLODNY and has shown this theory to be completely untenable. Preliminary reports have appeared in *Nature* (HATCHER and GREGORY, 1941; HATCHER, 1943). The auxin content was determined by the standard *Avena* coleoptile test of WENT (1928). The following salient points have been established. Mature cereal grains of different species vary considerably in total auxin content and concentration, giving a descending series: maize, oat, rye, wheat, barley. The auxin of the rye grain is located in the endosperm and chiefly in the aleurone: none could be definitely detected in the embryo itself. The auxin contents of spring and winter rye varieties are not different. The auxin is detectable in the embryo either during development or during germination either at normal or vernalizing temperatures. Auxin, far from being accumulated in the embryo of grain undergoing vernalization as CHOLODNY supposed, is not concerned in the process. The other findings in this work are not of immediate concern and are therefore very briefly mentioned.

Free auxin appears in the rye grain in the third week after fertilization, accumulates during the next month to a peak value and disappears almost completely with ripening. A "precursor" is present similar to that described in maize by AVERY, BERGER, and SHALUCHA (1941) and isolated by BERGER and AVERY (1944). This precursor releases indole-3-acetic acid on alkaline hydrolysis (optimal conditions N/50 NaOH). The precursor and free auxin appear at the same time and both accumulate to a peak value, up to which time they are present in a constant ratio of 2:1. During ripening the free auxin disappears at a greater rate, so that in the ripe grain of rye the ratio reaches a value of 80 : 1 precursor to free auxin. Spring and winter rye are quite similar in the matter of auxin production.

When prematurely harvested the same cycle of auxin accumulation and disappearance occurs, but the peak value is the lower the earlier the grain is removed from the plant. No auxin is present in the ear prior to emergence,

and is then first formed in the anthers, where a cycle of accumulation and disappearance occurs similar to that in the carpel.

The shortening of the first leaf after low temperature treatment noted by THIMANN and LANE (1938) referred to above, and held by them to support CHOLODNY's hypothesis, has been shown to be quite independent of the vernalization process, for it occurs equally in spring and winter rye and is a different effect of low temperature.

It has not been possible to deal in any detail with the differences of opinion between various workers regarding the question of reversibility of vernalization. It has already been noted that plants have been successfully "devernalized" by drying, or by exposure to high temperature or to anaerobic conditions. The latest and confirmatory experiments on devernalization by high temperature are reported by PURVIS and GREGORY (1945). Petkus winter rye was vernalized for 42 days at 1°C. and the seeds were then subjected to a range of temperatures for varying periods of time (temperatures, 25°, 30°, 35° and 40°C.; durations, 1, 2, 3, 4, 5, 6 and 10 days). Petkus spring rye was subjected to similar heat treatments without previous low temperature treatment. Results obtained at 35°C. are given in table where 'scores' give a positive measure of the degree of vernalization; other results will be later published in full (the method of scoring is described by GREGORY and PURVIS, 1938*a*).

	SPRING RYE (UNVERNALIZED)		WINTER RYE (VERNALIZED)	
DURATION OF HEAT TREATMENT	'SCORE'	NO. OF REPLICATES	'SCORE'	NO. OF REPLICATES
0 (Controls)	123 ± 0.12	(52)	100 ± 3.0	(47)
8 hours	120 ± 0.77	(48)	95 ± 4.6	(44)
16 hours	121 + 0.93	(53)	90 ± 4.9	(35)
1 day	120 ± 0.65	(62)	75 ± 6.5	(35)
2 days	121 ± 0.68	(47)	80 ± 5.9	(39)
3 days	124 ± 0.40	(55)	72 ± 9.5	(16)
4 days	123 ± 0.46	(49)	72 ± 6.4	(33)
5 days	120 ± 0.64	(42)	63 ± 6.6	(35)

PURVIS and GREGORY drew the following conclusion from these data:

(*a*) Heat treatment of the seed is without effect on the flowering behaviour of spring rye, thus showing that there is no question of a lethal action. Spring rye heated at 40°C. for 4 days scored 120, substantially the same as at 35°C. The reduction in score in winter rye is therefore not due to any injury effect, as is claimed by investigators who believe that vernalization is not reversible.

(*b*) A progressive and significant reduction in the score accompanies prolonged heat treatment of winter rye. The delay in flowering is then due presumably to the reversal of the vernalization effect. Complete devernalization did not occur. After treatment at 40°C. for 2 days the score was 79 ± 8.0 (four times that of unheated and unvernalized winter rye) whereas a further day at 40°C. killed all the seed.

In the same experiment, after the preliminary vernalization for 42 days at 1°C. and the subsequent heat treatment as above, the seeds were then revernalized by exposure to low temperature for a further 6 weeks. The effect on ear development is shown in the following table.

Duration of heat treatment	'Score'	No. of replicates
0 (Controls vernalized 12 continuous weeks at 1°C.)	112 ± 1.18	(17)
8 hours heating followed by six weeks at 1°C.	113 ± 0.95	(48)
16 hours	117 ± 0.82	(41)
1 day	117 ± 0.45	(42)
2 days	113 ± 0.93	(39)
3 days	118 ± 0.65	(54)
4 days	117 ± 0.63	(54)
5 days	116 ± 0.65	(55)

The scores are slightly higher than those of the control series vernalized for 12 weeks continuously, thus proving reversibility of the vernalization process in both directions. The efficacy of the high temperature devernalization in these experiments depends upon the duration of the previous low-temperature period and thus upon the "intensity" of vernalization; this aspect is now being investigated.

Field experiment at East Malling Research Station, 1942. — Soviet research on vernalization had indicated that increases in yield could be obtained with spring cereals, and techniques for the treatment of spring cereals were included by Lysenko (see I.A.B. 1935) and Dolgušin (ibid.) in their recommendations to agronomists. The requisite temperatures varied with the type of cereal used: thus 0-2°C. was suggested for winter wheat and barley; 2-5° for hard late wheats, spring barley, and oats; and 10-12°C. for soft spring wheat and hard early wheat. The duration of vernalization recommended varied from 35-40 days for winter wheat, to 5-7 days for early spring wheat.

In the field experiment under discussion (Gregory, 1945), two each of the cereals wheat, barley, and oats were used. Vernalization treatments were used covering the range of temperatures recommended by the Soviet agronomists, and at each temperature two durations, one long and one short, were employed.

The varieties used and the vernalization treatments given are stated below:

	Variety:
Wheat	Little Joss, April Bearded.
Barley	Plumage Archer, Spratt Archer.
Oats	Victory, Resistance

Temperature:	Duration of vernalization in weeks:
37°F.(2.8°C.)	4 and 2
40°F.(4.4°C.)	3 and 2
45°F.(7.2°C.)	3 and 2
50°F.(10°C.)	2 and 1

Sowing date (1) April 6-11; (2) May 4-9.

There were thus, in all, six varieties with four vernalization temperatures each with two durations of treatment and in addition two controls. The

F. G. Gregory, distinguished British plant physiologist, of the Imperial College of Science and Technology, London.—*Photograph by J. Russell & Sons.*

O. N. Purvis of the Imperial College of Science and Technology, London.—*Photograph by E. C. Thompson.*

Field Trials carried out by Gregory and Purvis at East Malling, described on pp. 26–28, showing the cereal plots, unvernalized in centre, vernalized at left and right.

whole experiment was carried out with two sowing occasions. Each treatment was replicated eight times giving in all ($6 \times 10 \times 2 \times 8$) 960 plots. A factorial design was used for the experiment which covered an area of approximately 0.6 acres. As the results are shortly to be published in full, only a brief summary is given here.

The variety, Little Joss wheat, was found to behave like a winter wheat and showed a very large response to vernalization as seen from the table.

Yield of Grain and Straw for Little Joss Wheat in cwt. per acre:

Temperature of vernalization	Duration of treatment		Duration of treatment	
	Long	Short	Long	Short
	Grain		Straw	
37°F.	17.5	10.7	33.2	28.2
40°F.	17.0	11.6	35.1	28.0
45°F.	13.1	12.0	30.2	27.0
50°F.	6.9	6.1	22.9	22.9
Control (unvernalized)	3.5		22.7	

The effect in the true spring varieties of the vernalization treatments on grain yields are given in the table below.

Effect of Treatment on Grain Yield in cwt. per acre in True Spring Cereals: —

Variety	Vernalized	Control	Difference
April Bearded	21.5	21.1	$+0.4 \pm 0.73$
Plumage Archer	28.2	25.8	$+2.4 \pm 0.90$
Spratt Archer	24.8	22.3	$+2.5 \pm 1.19$
Victory	19.9	18.9	$+1.0 \pm 0.86$
Resistance	23.6	23.1	$+0.5 \pm 0.97$
Mean of all varieties	23.6	22.2	$+1.4 \pm 0.42$

With each variety vernalization has led to an increase in grain yield, but only in the case of the two barley varieties are these increases statistically significant. The mean effect of vernalization on all varieties combined is about 5 per cent and is significant. The mean effects of temperature of vernalization on grain yield combining all varieties used were:

37°F. 23.5 cwt.; 40°F. 24.0; 45°F. 23.3; 60°F. 23.6.

There is no suggestion of an optimal temperature of vernalization, and consequently no support can be found in this experiment for the view that spring cereals require higher temperature than winter cereals during vernalization, as Lysenko recommended. Nor is there any evidence that shorter durations are more effective; the mean grain yield for long duration being 23.2 cwt. and short duration 23.8 cwt.

Observations were made during the course of the experiment on ear emergence in the true spring cereals; only a small effect of vernalization was

recorded, ranging from less than 1 day above the controls in Plumage Archer barley to 4 days in Resistance oats. This acceleration in ear emergence although statistically significant is too small to be of practical importance in the climate of Great Britain. A small effect of vernalization was noted on the total number of ears produced, but this was not consistent among the varieties used, some giving an increase, others a decrease, so that the mean overall effect was not significant.

This experiment, in which a high order of accuracy was attained (S.E. of mean yield per acre less than 2 per cent of the mean), showed an effect of vernalization on grain yield not exceeding 10 per cent in the barley varieties, 5 per cent in the oats, and no effect on spring wheat, and of these results only those with spring barley attained statistical significance.

United States of America: — Reference has already been made to the review on vernalization published by McKinney (1940). The author noted that the majority of investigations outside Russia fail to recognize any great commercial gain to be derived from the application of vernalization to the small grains, rice, maize, sorghum, forage crops and cotton in the regions where these crops are adapted. McKinney believes the general opinion to be that the crop problems can best be solved through developing more adapted genotypes. Some commercial value is attached to the chilling method when used to force flowering in daffodils, Dutch and Spanish iris, and Easter lily. Apart from possible application to seed production in biennials, or in speeding up seed production in genetical and general crop improvement studies, McKinney considers that the relation between temperature, photoperiod, intensity and quality of light must be fully understood before satisfactory results can be obtained from the initial chilling.

McKinney and Sando (1933) themselves conducted experiments on earliness and seasonal growth habit in wheat, finding that sexual reproduction can be greatly accelerated by first subjecting the slightly germinated seeds of winter wheat to low temperatures in the dark for 50 to 65 days before sowing. By growing plants from treated seed subsequently at higher growing temperatures in a long day, it is possible to obtain two or more crops of winter wheat in a year, according to the variety.

Seasonal growth habit in wheat is considered as an aspect of earliness and lateness. So far as earliness is concerned, McKinney and Sando state that the winter varieties have low temperature and short-day optima during the initial growth phase, whereas spring varieties have optima at the higher temperatures and the longer photoperiods. "Earliness and lateness of sexual reproduction appear to depend on the interrelation of several characters such as the number of internodes per culm, the growth rate of the internodes, the duration of the elongation of the internodes, and environmental-response characters which influence the expression of these characters." In relating environmental response to number of internodes, McKinney and Sando forecast the number-of-leaves interpretation put forward by Gregory and Purvis.

Lojkin (1936) succeeded in vernalizing Turkey Red and Leaf's Prolific wheat by exposure to temperatures of 1 to 3°C., but low temperature did not shorten the vegetative period of the spring cereals, Blue Stem wheat

and Clydesdale oats. Drying the vernalized seeds and exposing them to warm temperatures decreased or nullified the vernalization already produced.

The location of the American sugar beet seed industry in areas where thermal induction, that is, vernalization in the field under the natural environment, is guaranteed, is an interesting example of the practical application of this type of research. Details are given in Chapter 18 of Crop Production and Environment (WHYTE, 1946).

India: — Agricultural physiologists in India have shown much interest in the developmental physiology of the crops grown in that country, and a clear appreciation of the problems at issue in the study of the relations between growth and development. For example, the degree of interest is indicated by the fact that a discussion on vernalization was held by the Imperial Council of Agricultural Research in December, 1939, at which it was emphasized by some of the attending physiologists that (*a*) experimental data must be obtained to discover whether particular strains of a selected crop will or will not respond to vernalization; (*b*) to obtain this information experiments with different strains should be undertaken in different regions; and (*c*) a study of the effect of the prevailing after-sowing environmental factors of given regions on the life cycle of both vernalized and untreated seeds is essential in order to evaluate the practical possibilities of the method for Indian agriculture. In discussing the question of practical application, SEN (1940) reviews some technical aspects which will require to be considered before the method can be expected to become part of the routine agronomic practice of India. It is not anticipated that Indian cultivators will master vernalization on their own, and SEN suggests that a central station for vernalization should be opened, as most seeds can be dried, stored and distributed after vernalization without suffering damage.

It is a well-known part of the vernalization technique that a certain minimum amount of germination (growth) is essential before vernalization can be effective. When vernalizing mustard, one of the Indian crops on which experiments have been made, this period has to be watched very carefully, as only *unsplit* vernalized seeds can have any practical value (SEN and CHAKRAVARTI, 1942). Sprouted chilled seeds have to be sown very carefully as drying is fatal for them; unsplit seeds can be dried and stored without losing their subsequent germinating capacity. Having found that vernalized seeds of mustard produce plants which flower significantly earlier (SEN and CHAKRAVARTI, 1938), these workers in the United Provinces of India made subsequent experiments for 4 years to discover (*a*) the optimal conditions and period of chilling necessary to induce maximum vernalization in unsplit chilled seeds, (*b*) response of different strains, (*c*) effect on progeny, (*d*) period for which unsplit chilled seeds can be dried and stored without reversal of vernalization, and (*e*) the effect of the temperature and daylength subsequent to sowing on the developmental physiology of plants from vernalized and control seeds.

The technique of vernalization used by Russian and other workers has been fully described elsewhere (I. A. B. 1933, 1935) ; it may be of interest to describe the technique used under Indian conditions by SEN and CHAKRA-

VARTI (1942). The following quotation applies to large samples, that for small samples having already been described earlier (1938).

For these larger samples modifications were introduced, particularly in regard to the containers of seeds and provision for absorption of CO_2 from the respiring seeds. The seeds to be chilled are first soaked under excess of water to induce them to absorb about 60 per cent of their weight of water, a procedure which generally requires 6 to 8 hours, according to the room temperature. After removal of excess water by spreading the seeds over several layers of absorbent cloth, they are placed in muslin bags or unglazed porcelain pots of suitable sizes and then placed inside the moist chamber of the chilling cabinet.

Any watertight box of required dimensions with removable lid can be used for a moist-chamber. When boxes of thin wood are used, they should be thoroughly asphalted inside and out. The inside of the box is lined with blotting paper and sufficient water is placed at the bottom of the box to maintain the absorbent lining moist throughout the period of chilling. For absorption of CO_2, a concentrated solution of potassium hydroxide is kept at the bottom of the box in a large, flat porcelain dish, the rim of which is previously paraffined to prevent creeping of KOH solution. A removable thick wire-net frame is placed over the KOH dish to protect the seeds against any accidental contact with the solution. Seeds in bags are suspended from hooks screwed on to the removable lid of the box, care being taken to see that the suspended bags do not touch the wire-net guard, or the moist blotting-paper lining of the box. When unglazed porcelain pots are used as seed containers, they are placed on the wire-net guard above the potash solution. From daily readings of the maximum-minimum thermometer, the temperature range to which the seeds are subjected is recorded. Obviously, from these readings no definite idea is obtainable about the duration of the recorded temperatures each day.

SEN and CHAKRAVARTI consider that an electrically operated cabinet of the Frigidaire type with an automatic device for maintaining a constant low temperature is undoubtedly the most suitable appliance for chilling seeds, but having no available electrical supply were themselves obliged to use a kerosene-operated Electrolux. An ordinary ice-box can be used, or even a wide-mouthed thermos-flask when the temperature required is not below 5°C. and only small samples of seeds are to be chilled. The thermos-flask is half-filled with freezing mixture and the soaked seeds are hung in a muslin bag from a hook screwed on the underside of the cork stopper of the flask. The process of daily renewal of the freezing mixture ensures the necessary removal of CO_2 and a supply of fresh air. Additional moisture when required can be given to the seeds by dipping the bags in ice-cold water; the excess water automatically drips down into the flask.

After the required periods of chilling, any mustard seeds which may have sprouted are discarded and the unsplit seeds are washed and dried at room temperature until they attain a constant weight. This period varies in the United Provinces from 3 to 5 days, according to the season. The seeds are then packed in a sealed container and stored inside an Electrolux.

All five strains of mustard vernalized by SEN and CHAKRAVARTI responded to the treatment, the degree of response varying with variety.

Seeds which sprout as well as those which remain unsplit during the period of chilling are vernalized, but, for the same dose of chilling, plants from sprouted chilled seeds are earlier. The vernalization effect is not transmitted to the progeny. When growth of the embryo is successfully confined within the elastic limits of the seed coat, the unsplit chilled seeds can be dried and stored for long periods (at least 863 days) without any resultant devernalization.

It was found that the mustard Type 27 used in these experiments has no obligatory low-temperature requirement for the thermo-phase, plants from untreated seeds flowering even when the minimum night temperature is 20°C. or more. Partial natural vernalization can, however, be induced in Type 27 when the embryo develops under a low temperature, and artificial vernalization has its maximal effect in 6 weeks. Once the thermo-phase has been completed, mustard appears to develop towards maturity best in a photoperiod of 13 hours, with an optimal associated temperature of 30°C.

Following these experiments, other Indian workers at the Botany Dept., Presidency College, Calcutta (Sen Gupta and Sen, 1944) made observations on the effects of time of sowing, photoperiods and vernalization on the growth and development of the two varieties of mustard, Tori No. 7 and Rai No. 5. Finding no response to vernalization, it was stated that their results did not confirm those of Sen and Chakravarti. The latters' reply (1944) was to the effect that their own results applied only to the five strains tested. They considered that no definite conclusions by Sen Gupta and Sen are warranted because the maximum period of chilling they used was only 30 days. The fact that unsprouted soaked seeds were chilled at 2 to 4°C. for different periods does not in itself ensure that they were properly vernalized; the technique or the conditions following chilling have not been described, and the conclusions are based on data obtained from a single sowing of Rai No. 5 and Tori No. 7.

Other crops dealt with by physiologists in India include gram (*Cicer arietinum*), rice and wheat. Low temperature applied to gram at the time of germination accelerates subsequent inception of the reproductive phase, while high temperature definitely retards it. The degree of response in both cases is a varietal character (Pal and Murty, 1941). Pillay (1944) has reported a preliminary experiment to determine whether pre-sowing treatment with low temperature would induce earlier flowering and high yield in gram under the conditions of Orissa. Seeds of uniform size of the variety, Sabour Type 4, were soaked in water for 22 hours at room temperature. The smaller seeds were then placed in a Kelvinator at 0 to 2°C., one lot for 7 days and another for 14 days. The latter seeds produced plants which flowered only 3 days earlier than the controls, and there was no significant difference in dry weight of pods or of stems.

Much work has been done in the United States of America, Japan, India and other countries on the developmental physiology of rice, more particularly with regard to photoperiods. In addition, Indian and Russian workers write about the vernalization of rice by short day or temperature. Using the former treatment in Bengal, Sircar and Parija (1945) obtained results of agricultural importance with a winter variety of rice, "Rupsail." The time to flowering of this variety has been reduced from 133 to 47 days

by "vernalization by short days." This is thought to be the shortest period yet reported within which winter varieties of rice will flower. ALAM (1940/41) had already concluded that all varieties require a minimum period of 30 days for vegetative growth and a subsequent period of about 30 days of exposure to short days for flowering. This acceleration claimed by SIRCAR and PARIJA is applicable to the cultivation of rice in Bengal. A variety of fine rice could be grown in a much shorter time; by inducing early maturity it could escape flood; early harvesting would leave sufficient time for preparation of fields for subsequent crops in the rotation.

Two experiments on vernalization of rice by temperature may be noted. PARTHASARATHY (1940) vernalized sterilized seeds in darkness or continuous light at 10 to 20°C. for three weeks. Those vernalized in darkness flowered 4 to 5 days earlier than the control. SKRIPČINSKIĬ (1940) obtained a distinct response from one variety only, British India 1220, in tests made for 3 years at the Rice Testing Station, Krasnodar. This variety eared 10 days earlier after vernalization at 6 to 8°C. and 8 days earlier after vernalization at 15 to 17°C. than the control plants grown in short day.

In addition to experiments on the relation between light and temperature and the course of development, Indian workers have also adopted a special pre-sowing treatment for inducing or increasing drought resistance. CHINOY (1942) developed the technique for wheat, and PARIJA (1943) has applied it to rice; water requirements for the treated plants were significantly less than for the control plants and the yield of grain significantly greater when the interval of watering is 8 days. Similar experiments have been made with jute, the effects of alternate moistening and drying and after-sowing light conditions being observed on drought resistance and earliness of flowering (KAR, 1944). There was an increased resistance to drought after treatment, but the earliness observed was due to the photoperiods following sowing.

PAL and MURTY (1941) state that, although low temperature at the time of germination may be indispensable for the normal development of English winter wheat, Indian wheats come into ear (without chilling) even at high summer temperatures, indicating that low temperature is not indispensable. A further indication that Indian varieties have little if any requirement of low temperature, but that response to light can be readily obtained is also seen in the experiments of KAR (1940).

SEN and CHAKRAVARTI (1945) have been testing the response of wheats to vernalization since 1938. The non-Indian varieties, Holdfast, Little Joss, Yeoman, Juliana and Yorkwin have been used, and significant responses have been obtained, that is, earlier emergence of the inflorescence in plants from pre-chilled seeds. Results of attempts to vernalize Indian varieties of wheat in different parts of India have led to the general acceptance of the fact that the cultivated strains of Indian wheat will not respond to vernalization because of their shorter life cycles. SEN and CHAKRAVARTI have, however, found that a very good response was obtainable in the first, second and third generation hybrids made by them between T.P. 4 (Indian wheat) and Yeoman (Cambridge winter wheat). Further trials have shown that a response can be obtained in a number of pure strains of cultivated Indian wheats and have now led to a systematic

study in collaboration with Dr. B. P. Pal, Imperial Economic Botanist, of the vernalization response of all the available strains of Indian wheats in his collection. A report will shortly appear in a joint paper with B. P. Pal of the results of vernalizing 150 strains of Indian wheats. Though an earliness of agricultural significance in ear emergence of certain cultivated Indian wheats can be obtained by the use of vernalized seeds, it is found that the number of tillers, the factor positively correlated with yield, is smaller. Trials on closer spacing in sowings are therefore being made.

Response to Temperature Before Seed Ripening: — The discovery reported independently by Kostjučenko and Zarubaĭlo in Russia and Gregory and Purvis in England that the low temperature effect associated with vernalization can be obtained on ripening seeds while they are still attached to the mother plant has made it desirable to give careful consideration to the environment, and particularly to the temperatures experienced before harvest.

Kostjučenko and Zarubaĭlo (1935, 1936, 1937) laid down a trial of winter wheat varieties at the Polar Experimental Station of the All-Union Institute of Plant Industry (VIR) at Hibiny. The grain used had been grown in two widely differing environments, namely, Hibiny itself (N. Lat. 67°44′) and Kirovobad (N. Lat. 40°41′). In both sowings vernalized and unvernalized grains were used. In September of the sowing year it was seen that the plants grown from these grains of different origin were distinct in their behaviour. Plants from Kirovobad grain artificially vernalized were then at the milk-ripe stage, while those from unvernalized Kirovobad grain were at the tillering stage. On the other hand, plants from Hibiny grain also artificially vernalized were almost at the stage of wax ripeness, while plants from the same grain not artificially vernalized exhibited partial or complete flowering; some of the latter had set seed in the ears of the main stem.

Thus, these Russian varieties of wheat, generally regarded as winter forms, behaved as spring forms when grown from grain which had ripened at Hibiny, but retained their winter habit when grown from Kirovobad grain. Kostjučenko and Zarubaĭlo conclude that the Hibiny grains had been able to pass their "stage of vernalization" or thermo-phase under the natural conditions of these northern latitudes, while the Kirovobad grains had not done so and still required artificial vernalization before they could reach maturity in one season after being sown in spring. It was assumed that the embryos of the Hibiny grain were vernalized by low temperature while still attached to the mother plant. An embryo which has not entered the dormant state may be sensitive to vernalization in the same degree as one which has been brought from the resting non-reactive condition by soaking. The details of these and other experiments by these Russian investigators are discussed more fully elsewhere (Whyte, 1946).

After their experiments on the vernalization of excised embryos, Gregory and Purvis (1936*b*, 1938*a*) proceeded independently to study the effect of vernalization on developing embryos and immature ears. Having shown that the vernalization process occurred in the embryo apart from the endosperm, it appeared possible to apply the low-temperature treatment

after anthesis, while the embryo is developing, and before the onset of dormancy.

A preliminary experiment was performed in 1935, when the ripening ears were chilled by two methods:

(*1*) The ears together with several nodes of the stem were cut off and kept in water in a refrigerator for 5 weeks at 1°C. Control ears similarly treated were kept in a dark room at normal temperature until the grain ripened off. After the low-temperature exposure the treated ears were allowed to complete ripening at room temperature.

(*2*) The second method consisted in treating ears attached to the plant. The selected ears after anthesis were inserted into wide glass test-tubes, plugged with cotton wool. In one set these tubes were placed in the necks of vacuum flasks containing crushed ice. The ears were thus kept at low temperature but did not come into contact with free water. Control ears were similarly treated and placed in vacuum flasks but without ice. After 24 days the ears were removed and allowed to ripen normally in the open air.

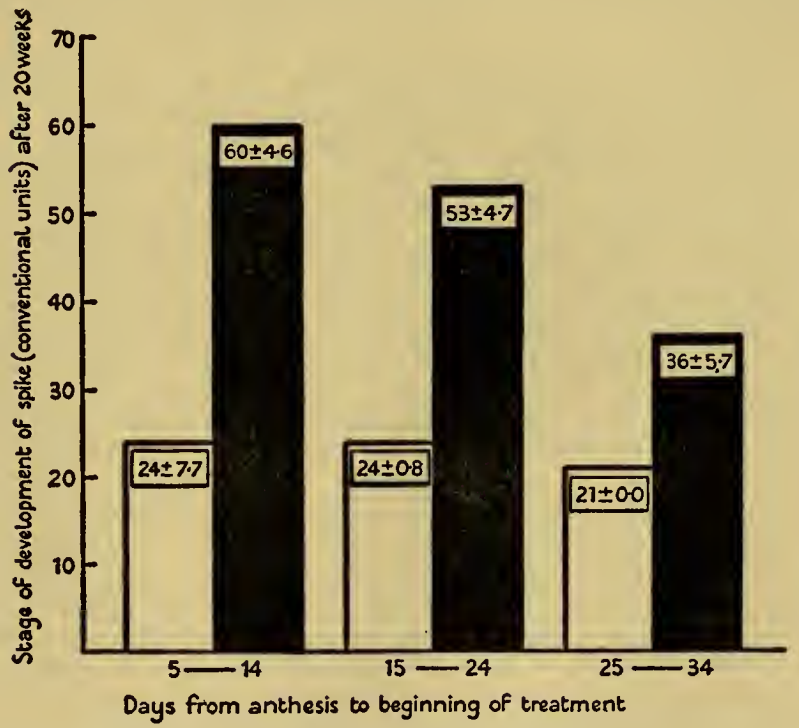


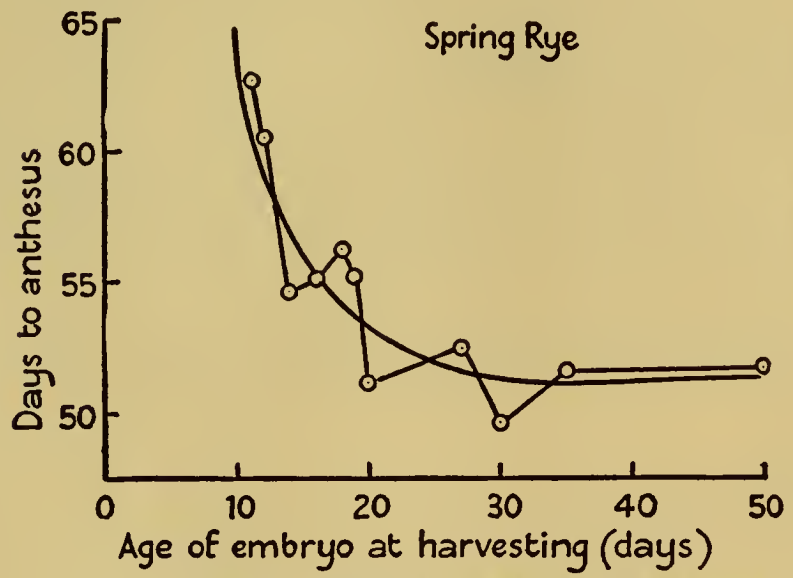
Illustration from Gregory and Purvis' classic 'Studies in the Vernalization of Cereals' (II, The Vernalization of Excised Mature Embryos, and of Developing Ears, *in* Ann. Bot., N. S. 2, 5, 1938) showing the relation between age of embryo at beginning of vernalization in the ear, and effectiveness of the treatment (black = vernalized; white = unvernalized controls).

The ripe grains obtained from plants thus treated in 1935 were sown on March 17, 1936, in pots of sand, without further low-temperature treatment. Flowering was irregular, especially in those plants resulting from grain which had been treated in vacuum flasks, where the duration of the treatment was less than that known to be optimal for vernalization, but flowering was appreciably hastened by both methods of chilling and results were sufficiently encouraging to warrant repetition of the experiment in the following year, when longer periods of treatment were used.

Effect of Vernalizing Developing Ears of Petkus Winter Rye 1935: —

Method of treatment	Time of treatment	Days from planting to anthesis in resulting plants.	
		Ripened at 1°C.	Ripened at normal air temperature
Cut ears in water	5 weeks	102	146
Attached ears in vacuum flasks	24 days	110	164

When a larger number of ears was treated in 1936, the ears were placed in a refrigerator while still attached to the stem, and in some cases whole plants were treated in this way. The period of chilling was increased to 45 days, and final ripening was carried out at medium temperatures. The ears were air-dried and the grain sown on May 31, 1937, without further treatment with low temperature.



Text-fig. 2. Spring rye. Relation between age of embryo at harvesting and time to anthesis in resulting plants.

Another figure from Gregory and Purvis' article referred to on opposite page.

Vernalization of Growing Embryos in the Developing Ear of Petkus Winter Rye, 1936: —

Treatment	No. of Plants	Stage of flower initiation	Condition of plants 15 weeks after planting	
			Stage of fully formed ears	Maturity in conventional units
Vernalized	156	65 per cent	38 per cent	53
Control	49	49 per cent	0 per cent	24

Reference should be made to the original article for the method of measuring maturity in conventional units. It is clear from these results that the low temperature during the previous season had a marked effect, although GREGORY and PURVIS note that not all the treated grains had attained the vernalized condition. Only 38 per cent of the treated grains produced plants with fully emerged ears, although others were approaching that stage. These data led to the same conclusion as that reached by KOSTJUČENKO and ZARUBAĬLO with regard to the sensitivity of an active embryo and the insensitivity of a dormant one.

GREGORY and PURVIS (1938*a* and *b*) dated the ears at anthesis and thus determined the age of the treated embryos. The results of the experiment showed that they could be grouped into 10-day classes covering the period from 5 days to 35 days after anthesis. The treatment is effective from the earliest stage of the development of the embryo, decreasing in intensity as beginning of treatment is delayed. Low temperature is therefore effective only while the embryo is actively growing, and ceases to be operative when the embryo becomes dormant. GREGORY and PURVIS conclude that the effect is quantitative, depending on the duration of the exposure to low temperature as had been shown to be the case in normal vernalization (PURVIS and GREGORY 1937).

An important result which probably indicates how early a developing embryo is fully sensitive to environmental conditions is that obtained by GREGORY and PURVIS (1938 *a* and *b*), who showed that seed obtained from ears removed from the parent plant as early as 5 days after anthesis germinated after being sown in the following spring. Completely normal plants were produced, although the individual immature grains were very small (4×1 mm.) and had apparently no reserves.

When winter rye was used, the plants grown from seeds having a range of maturity of 5 to 50 days showed no difference in the stage of development reached after 17 weeks. As the plants had not been vernalized, no ears emerged. In spring rye, on the other hand, a variation was found in the days from germination to anthesis varying from 51.8 ± 1.17 days (mean of ten plants) in completely matured seeds, to 62.7 ± 0.91 days (mean of three plants) in grain from ears removed 11 days after anthesis, the earliest removed ears to give viable grain. A decrease in the time taken to flower is correlated with maturity of the ripening grain. GREGORY and PURVIS suggest the possibility of partial devernalization of the very immature grains of spring rye.

Later studies made at the Research Institute of Plant Physiology, London, have been concerned with a more detailed investigation of the processes occurring in the embryo-sac of a cereal subsequent to fertilization, and of the conditions of formation and the subsequent growth of dwarf embryos of rye. NUTMAN's account of the former investigation (1939) is concerned with the anatomical and cytological evidence for the formation of growth-promoting substances in the developing grain of rye.

In a later paper NUTMAN (1941) describes the formation of the dwarf grain of rye in ears harvested at an immature stage, and compares the morphology and anatomy of dwarf and normal grains and embryos. He confirms observations made by GREGORY and PURVIS with rye, and earlier by

HARLAN and POPE with barley (1922, 1926) that ears removed from the plants as early as 5 days after fertilization produce viable grain.

Conclusion: — It has been seen that research on the biological processes concerned in vernalization has almost reached its limit in the meantime, particularly in the very detailed studies of GREGORY and PURVIS. Until their hypothetical precursor has been isolated and its nature defined, striking advances in this direction are not to be expected.

Neither does it appear probable that the method of vernalization will itself become widely used, except possibly in those districts in countries such as the U.S.S.R. or India where conditions of drought or flood make a difference of a few days in maturity a desirable objective. In countries not experiencing extreme conditions, the low-temperature treatment will not be used when superior genotypes can be found, and would therefore be confined to genetical or similar research, or in the production of market garden crops if a few days' earliness means increased economic return.

The greatest economic significance of this research appears to be, however, in the two incidental discoveries which have been made, namely, the possibility of vernalization before seed ripening and of devernalization and revernalization according as conditions favour one process or the other. Vernalization of developing embryos while still attached to the mother plant is an important factor in the selection of areas for seed production, and in plant introduction and the moving of seeds from one environment or latitude to another. Early strains may become late, and vice versa.

Devernalization also affects a number of agronomic questions, as in many environments a temporary period of high temperature may partially or completely annul any degree of vernalization already achieved naturally in the field. Waterlogging of a field in a wet winter might also be expected to produce the anaerobic conditions found to favour devernalization; seeds in a heavy clay soil may possibly be more liable to devernalization through anaerobic conditions than those in light well-aerated soils.

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HISTORY OF RESEARCH IN PHOTOPERIODISM

by

A. E. MURNEEK

University of Missouri, Columbia, Missouri

Introduction: — In their growth and development plants are affected by many environmental factors. Some of these are under the control of man and form a basis for cultural practices in crop production. One of the latest major external factors discovered is the length of day, technically known as the *photoperiod.* The vast majority of plants probably are sensitized to various degrees, through natural or artificial selection, and react to recurrent diurnal light periods. This response to the photoperiod is called *photoperiodism.*

While the day length may modify any and all structural parts of a plant, our interest, from the beginning of the disclosure of this phenomenon till today, is centered primarily on its influence on the formation of flowers and development of fruits and seeds. This is but natural, for this particular function of the plant is closely associated with, if not basic for, the successful production of many economic crops.

The influence of length of day is modified, and sometimes counteracted, by other environmental factors, particularly temperature. For this altered or dual effect the term *thermophotoperiodic induction* has been proposed. In cases where the development of a plant is affected by diurnal alterations in temperature, somewhat analogous to that in other plants by photoperiod, one may possibly speak of *thermoperiodicity.*

Variability in response to the photoperiod of various species and varieties points clearly to a genetic mechanism in operation in bringing about this phenomenon. Active selectional processes, in this respect as in many others seem to be at work in the intricate economy of living organisms towards adaptability to the environment. In the case of domesticated species, man often participates as an operating agent in the selection, preservation, propagation and multiplication of many photoperiodically adapted varieties and strains. If necessary, through selection and hybridization, it is possible to impart desirable characteristics in this respect to plants hitherto not possessing them.

Photoperiodism, in relation to vegetative growth and sexual reproduction, is but a phase of the general problem of plant growth and development. The early investigators in this field were KLEBS in Germany (1903-1918) and LYSENKO in the U.S.S.R. (1928-). KLEBS initiated research work on developmental physiology of plants and demonstrated by various experimental procedures that structural changes, with special reference to reproduction, are not of an unalterable nature and, therefore, not due entirely to an "internal hereditary rhythm." They may be modified drastically, or even suppressed, by changing certain environmental factors, such as light, temperature or nutrition. LYSENKO, while known chiefly for his discovery and application of seed vernalization to hasten reproduction, has postulated the now popular theoretical concept of "phasic development of plants." Both the temperature and the photoperiod constitute two of the most important environmental factors affecting growth and development, as conceived by LYSENKO and later elaborated by his co-workers. A detailed discussion of contributions of the Russian investigators and others on this subject will be found in WHYTE's chapter on "History of Research in Vernalization."

Terminology: — To prevent a possible confusion in the use of certain technical terms and phrases in connection with the discussion of photoperiodism and related subjects, it is thought desirable to present herewith a list of the more popular terms with their definitions.

Photoperiod — Length of daily exposure to light (GARNER and ALLARD).
Photoperiodism — Response of plants to photoperiod (GARNER and ALLARD).
Photoperiodicity — Response of animals to photoperiod. Used by some zoologists (BISSONETTE).
Long-day plants — Species, varieties and strains in which the flowering period is accelerated by a relatively long daily exposure to light, usually more than 12 to 14 hours (GARNER and ALLARD), or which require minimum photoperiods or continuous light, but not darkness (LYSENKO), or which require short dark periods (HAMNER).
Short-day plants — Species, varieties and strains in which the flowering period is accelerated by a relatively short daily exposure to light, usually less than 12 to 14 hours (GARNER and ALLARD), or which require photoinductive cycles containing photoperiods of minimum intensity and dark periods of minimum duration (HAMNER).
Day-neutral (indeterminate) plants — Species, varieties and strains in which flowering is not influenced by length of daily exposure to light (GARNER and ALLARD).
Photoperiodic induction — Formerly, the carry-over effect of a photoperiod conducive to sexual reproduction to one opposite to it (LUBIMENKO and ŠČEGLOVA). Now, the stimulation of flowering by exposure to photoinductive cycles (HAMNER).
Photoperiodic after-effect — The same as photoperiodic induction (MAXIMOV). Plants may exhibit also temperature and possibly other "after-effects."
Photoperiodic adaptation — The adaptation of plants in their native or artificial habitat, to a definite length of day or to latitude (LUBIMENKO).
Photoperiodic inhibition — Inhibition or retardation of growth primarily of the main axis, by certain photoperiods (MURNEEK).
Photothermal induction — The induction of reproduction by a combination of photoperiods and temperature (OWEN *et al.*).
Thermo-photoperiodic induction — The same as photothermal induction (WHYTE).
Thermoperiodicity — Response of plants to alterations in day and night temperatures (WENT).
Thermoperiodic adaptation — The adaptation of plants, in their native or artificial habitat, to specific temperature requirements (LUBIMENKO).

Reviews on Photoperiodism and Related Subjects: —For a more detailed discussion of literature on photoperiodism in plants, and subjects appertaining thereto, than is possible to present here, the reader is referred to the following comparatively recent reviews:

General: —
GARNER, W. W. Biol. Effects of Radiation, Ch. 19, 1936 and Bot. Rev. 3:259-275, 1937.
BURKHOLDER, P. R. Bot. Rev. 2: 1-52, 97-168, 1936.
GREGORY, F. G. Sci. Hort. 4: 143-154, 1936.
BOWMAN, E. T. Journ. Austral. Inst. Agr. Sci. 4: 25-32, 1938.
TINCKER, M. A. H. Sci. Hort. 6: 133-149, 1938.
HAMNER, K. C. Ann. Rev. Biochem. 13: 575-590, 1944.
Sex expression in plants: —
LOEHWING, W. F. Bot. Rev. 4: 581-625, 1938.
Nutrition in relation to photoperiodism: —
MURNEEK, A. E. Mo. Agr. Exp. Sta. Res. Bul. 268, 1937.
MURNEEK, A. E. Growth 3: 295-315, 1939.
LOEHWING, W. F. Proc. Iowa Acad. Sci. 49: 61-112, 1942.
Temperature responses: —
THOMPSON, H. C. Proc. Amer. Soc. Hort. Sci. 37: 672-679, 1939.
Theories related to flower formation: —
ČAJLACHJAN, M. H. Hormonal theory of plant development, Moscow, 1937 (in Russian).
WHYTE, R. O. and OLJHOVIKOV, M. A. Chron. Bot. 5: 327-331, 1939.
CHOLODNY, N. G. Herbage Revs. 7: 223-247, 1939.
ADLER, F. Forschungsdienst 9: 332-367, 1940.

HAMNER, K. C. Cold Spring Harbor Symp. Quant. Biol. 10: 49-59, 1942.
Phasic development of plants: —
WHYTE, R. O. Biol. Revs. Cambr. Phil. Soc. 14: 51-87, 1939.
Anonymous. Herbage Revs. 7: 27-32, 94-95, 265-274, 1939; 8: 83-94, 1940.

Discovery of Photoperiodism: — The formative effects of diurnal length of exposure to natural light or artificial illumination have been observed, previous to the discovery of photoperiodism, by several investigators of plant growth and development (SCHÜBELER, 1880; KJELLMAN, 1885; BONNIER, 1895; TURNOIS, 1912). According to H. A. ALLARD (1944) an interesting reference to the photoperiod as affecting plants is given by A. HENFREY in his book "The vegetation of Europe," 1852, wherein a theorem is proposed that the length of day is a factor in the natural distribution of plants. KLEBS also, as early as 1913, seems to have had a fairly definite idea that the time of flowering of some of his experimental plants, *Sempervivum funkii,* was determined by the length of day. Not being able to secure flower development in winter by changes in nutrition, temperature, etc., KLEBS exposed them for a few days to continuous electric illumination. They produced flowers in the same greenhouse in which other non-lighted plants remained vegetative. Concluded KLEBS (1913):

"In der freien Natur wird sehr wahrscheinlich die Blütezeit dadurch bestimmt dass von der Tag- und Nachtgleiche (21 März) ab die Länge des Tages zunimmt, die von einer gewissen Dauer ab die Anlagen der Blüte veranlasst. Das Licht wirkt wohl nicht als ernährender Factor, sondern mehr katalytisch."*

To W. W. GARNER and H. A. ALLARD (1920), however, is due all the credit for the disclosure and demonstration of the phenomenon of photoperiodism. It was a real surprise to many investigators of plant life that so "dilute" an environmental factor as length of day has so potent an effect on many plants.

The early experimentation leading up to the crucial tests with tobacco and soybean plants are described by GARNER as follows:†

"The two cardinal observations with which we started were that, in contrast with other tobaccos, the new Maryland Mammoth variety always continued a purely vegetative type of growth through the open growing season at Washington, and that successive plantings of certain varieties of soybeans made at short intervals through the spring and early summer all tended to flower at the same date. In the case of tobacco, it was not at first realized that a seasonal effect was definitely involved in the very unusual behavior of the new variety. It was thought that perhaps the "shock" of transplanting to the greenhouse was a major factor, possibly aided by increasing age of the plants. We were temporarily misled by the observation that seedlings grown in small pots in winter and early spring flowered and fruited freely, thus suggesting a nutritional angle. The big lead came after several years with the observation that with the advance of spring new shoots developing on stumps that had been producing flowering shoots suddenly swung over to the indeterminate vegetative type of growth. It was then perfectly clear that a seasonal factor was involved. Since the plants were growing in a warm greenhouse, it appeared that temperature could be excluded. With respect to light, we naturally reasoned that intensity and composition might be involved. However, fairly extensive investigations were being conducted on other problems with both tobacco and soybeans that seemed to exclude intensity and spectral composition of light as important factors. At this stage the problem appeared to as-

* I wish to thank Dr. F. W. WENT of the California Institute of Technology for calling my attention to this reference.

† Private communication from DR. W. W. GARNER, Aug. 22, 1944.

sume a somewhat hopeless trend, but after much deliberation it was concluded that the only remaining seasonal phenomenon that could be a factor was change in relative length of day and night. The importance of this conclusion, of course, lies in the fact that length of day was dissociated from the factor of amount of solar radiation. The decisive test was then made in the simplest possible way but without great hope of success, mainly for the reason that there appeared to be no accepted basis in plant physiology for consideration of day length as other than a purely quantitative factor. Failure on the part of earlier workers to distinguish between *duration* and *amount* of daily illumination perhaps explains why photoperiodism was not discovered much earlier, for usually in reducing the hours of light the mistake was made of darkening the experimental plants in such a way as to subject them to two or more daily light periods. Ineffectiveness of mid-day darkening in inducing photoperiodic responses is brought out in the original paper (p. 574) and more fully developed in later articles."

While tobacco and soybeans were used largely in the preliminary trials, subsequently a wide variety of field, garden and ornamental plants were studied by GARNER and ALLARD (1920, 1923, 1930, 1940) as to their responses to photoperiods of various lengths. The effects on sexual reproduction were taken primarily into consideration, but much evidence was secured also on the influence of length of day on vegetative growth, such as increase in size of the plants, formation of bulbs and tubers, character and extent of branching, root growth, pubescence, pigment formation, abscission and leaf fall, dormancy and death. To this have been added by other investigators observations on the effects of the photoperiod on sex reversal, duration of the growth period and other phenomena (SCHAFFNER, 1923, 1930, 1935; KRAJEVOJ and KIRIČENKO, 1935; KRAMER, 1937; MANN, 1942; DANIELSON, 1945). GARNER and ALLARD, of course, noted that other environmental factors, such as light intensity, soil moisture and nutrients, etc., may and usually do modify photoperiodism in plants. It is significant that temperature was found most important in relation to the action of the light period on plant growth and development.

By the simple means of exposing only parts of a plant to definite photoperiods, GARNER and ALLARD (1923, 1925) were able to demonstrate with *Cosmos* that the response is largely localized. But the fact is pointed out that the determinative influence of the light period can be transmitted, in some cases at least, to other portions of the plant, as, for example, from the aerial parts to tubers of the potato. This was subsequently verified with several other tuber-bearing plants by RASUMOV (1931, 1935).

In his extensive work on photoperiodism in spinach KNOTT (1934) was led to the belief that the leaves appear to function in some way to hasten the photoperiodic effect in plants. Soon thereafter it was demonstrated by MOSHKOV (1935) and by ČAJLACHJAN (1936) and later by many others that leaves are the organs of perception of the length of day stimulus, whence it travels to the meristems and other parts of the plant. More recent evidence has shown that the youngest fully developed leaves are most sensitive to the photoperiod (MOSHKOV, 1937; PSAREV, 1937; ULRICH, 1939; NAYLOR, 1941).

Classification and Adaptation: — As regards their photoperiodism, plants have been classified by GARNER and ALLARD (1920, 1923) into short-day, long-day and day-neutral types. While this grouping is not fully acceptable in the light of our present evidence on plant development as af-

FIG. 1.—Original Maryland Mammoth tobacco plants with which photoperiodism was discovered. Plant on left grew in unlighted greenhouse (short days). Plant on right grew in electrically lighted greenhouse (long days). Winter, 1919.—Photo by GARNER and ALLARD.

FIG. 2.—Original Biloxi soybean plants with which photoperiodism was first demonstrated. Vegetative plants on left grew outdoors under natural long days. Reproductive plants on right grew outdoors under artificially shortened 10-hour days. Summer, 1920.—Photo by GARNER and ALLARD.

fected by light duration, it has been adopted by most investigators and is used widely.

In short-day plants flowering is induced experimentally by relatively short photoperiods, usually 10 hours or less; in long-day plants by photoperiods of 14 hours or more; and in so-called "neutral" plants by 10-18 hours of light duration or even continuous illumination (HARVEY, 1922). Examples of short-day plants are: Some tobaccos and soybeans, *Chrysanthemum, Salvia, Poinsettia, Cosmos* and many other of our spring and fall flowers. Of long-day plants there are: Spring varieties of cereals, spinach, lettuce, radish, potato, *Rudbeckia* and other summer flowers. Of neutral plants we have: Tomato, dandelion, buckwheat, cotton and some squashes and cucumbers.

Recently ALLARD (1938) and GARNER (1940) have added a fourth group, of which there seem to be a few representatives, designating it *intermediates*. They seem to flower at a day length of intermediate duration (12-14 hours), but are inhibited in reproduction by day lengths either above or below this length. Examples of such plants are: *Mikania scandens, Phaseolus polystachyus, Eupatorium torreyanum* and *Saccharum spontaneum*.

To lengthen the light period experimentally, GARNER and ALLARD found electric light of comparatively low intensity consistently effective for initiation or inhibition of reproduction or vegetation, depending on the type of plant treated. This has been fully verified by other investigators and is good evidence that, in general, intensity of the supplementary light used is not a factor in photoperiodism. Very weak light, of course, cannot be used, throughout the photoperiod for a large number of days without great disturbance in growth and development of plants.

Photoperiodism is an important factor in the natural distribution of plants. In their native habitats plants are adapted in various degrees to a variety of environmental factors, including the diurnal duration of light. They could not persist long in a specific region or extend their range unless the environment is favorable for some form of reproduction (POTAPENKO, 1945). Numerous observations have shown that genera, species and varieties have developed photoperiodic responses which enable them to adjust the time of flowering and fruiting (seed production) to definite seasons, characterized by certain lengths of day. Thus we have more or less typical spring, summer and fall blooming types of plants. The literature on this subject is voluminous, of which the following papers may be cited as examples: ADAMS, 1923; ALLARD, 1932; DARROW, 1934; DOROSHENKO, 1927; DOROSHENKO and RASUMOV, 1929; MCCLELLAND, 1928; MAXIMOV, 1929; TINCKER, 1925; KUZNETSOVA, 1929; LUBIMENKO and ŠČEGLOVA, 1927; ALLARD and ZAUMEYER, 1944; ALLARD and GARNER, 1940 and BÜNNING, 1943. Some synchronization to the seasonal photoperiod is remarkably close (SMITH, 1941).

In general, plants that have originated in southern or tropical latitudes will require short days for flowering, while those of more northern latitudes, roughly to the north of 60°, are long-day plants. When the latter are moved too far south, they will not produce blossoms. When carried farther north, they will still be reproductive, because of an increased photoperiod

and despite the shortened season. But southern plants are more difficult to adapt to northern latitudes where, due to the much longer days, they will continue to grow vegetatively till killed by frost.

Within specific groups of plants there may exist great variability as to their responses to definite photoperiods, even if attention is paid only to flowering and not to the earlier or later stages of the reproductive cycle. Thus within the genus *Phaseolus,* to three species of which (*P. vulgaris, P. lunatus* and *P. coccineus*) belong the beans commonly grown in the United States, there is a large number of varieties that are either short-day or day-neutral. But the Scarlet Runner bean, a variety of *P. coccineus,* is a long-day plant. Since most of the varieties of *P. vulgaris* and *P. lunatus* are day-neutral, they can be and are grown over a considerable range of latitudes. In fact, much of the varietal improvement in these two species has been associated with day-neutral characteristics (Allard and Zaumeyer, 1944). Analogous and possibly even more extreme situations are exhibited by soybeans (Borthwick and Parker, 1939; Rudorf and Schröck, 1941) and many other cultivated species (Beljdenkova, 1940; Goodwin, 1941; Laibach, 1940; Allard, 1941).

Among wild plants, or plants that have been domesticated but little, similar conditions seem to exist. Of the several instances that could be cited, it would seem to be sufficient to refer here to two recent studies. Olmsted (1944-1945) has investigated, both in the field and laboratory, the photoperiodic response of twelve geographic strains of side-oats grama grass (*Bouteloua curtipendula*). They were found to differ in their responses to the length of day, showing the existence of definite photoperiodic types within the species. Strains from southern Texas and Arizona consisted largely of short-day or intermediate plants, those from Oklahoma, Kansas and Nebraska included numerous long-day individuals, and those from North Dakota were made up chiefly of long-day plants. It is concluded that most specimens, within the twelve strains investigated, probably can develop flowers best on photoperiods existing in their native habitats. Whether this wide variability in response to the photoperiod is due to more or less stable inherited characters or is the result of heterozygocity, is not certain from the evidence presented. A similar situation seems to exist in other groups of plants (Rasumov, 1937; Kiričenko and Bassarskaja, 1937).

The adaptability to length of day of various species of the potato has been reported by Driver and Hawkes (1943). Though most wild South American potatoes were found to be short-day plants, certain clones of *Solanum andiginum, S. curtilobum* and *S. tenuifilamentum* appeared day-neutral, and one clone in each of the first two species reacted as long-day plants.

From these and other instances it is quite apparent that the present classification of plants on the basis of reactions of some members of the group, as regards sexual reproduction, to more or less definite photoperiods is not very appropriate.

In this connection there are other aspects of the problem of classification that should be taken into consideration. Very few species, excepting possibly those in equatorial regions and in the case of some desert, polar or high altitude ephemerals, seem to be adapted throughout their length of

sexual reproduction, from flower bud inception to seed maturity, to the same photoperiod or a combination of photoperiod with other environmental factors. In many plants flowers are initiated at one time of the year (one photoperiod) and their further development to anthesis takes place at another. It is highly probable that reproduction may commence by exposing experimental plants continuously to specific lengths of day but further development of floral organs may be curtailed or inhibited under this particular photoperiod. (Borthwick and Parker, 1939; Murneek, 1939). Disregarding equatorial regions, in nature most plants probably have adjusted themselves not to uniform diurnal periods of light but to continuously changing ones. It has been shown that many so-called short-day plants are really short-day → long-day plants as regards their response to photoperiods. Similarly quite a number of long-day plants are, in fact, short-day → long-day types. Hence, paradoxical as it may appear, there does not seem to be an essential difference between the two groups (Whyte and Oljhovikov, 1939).

Čajlachjan (1933) is of the opinion that classification of cereals into spring and winter types is unjustifiable in view of the fact that in any large collection strains exist within varieties, secured from different latitudes, that may be arranged in series, from spring to winter forms. Using certain species of *Poa, Digitalis, Trifolium, Pyrethrum* and *Hyoscyamus* as examples, Krier (1941) claims that there is no clear-cut distinction between winter and spring annuals, biennials and perennials. One type can be converted into the other under environmental conditions as determined by geographic location.

By considering two stages of reproduction only, flowering and fruiting, Eguchi (1937) recognizes the following classification, some representative plants for each being given by Loehwing (1939).

Optimal periods for:

Flowering: —	*Fruiting:* —	*Representative species:* —
Short	Long	Strawberry, *Cineraria*
Long	Long	Oxeye daisy, Spring barley
Long	Short	*Physostegia virginiana, Boltonia latisquama*
Short	Short	Soybeans, *Cosmos bipinnatus*
Long	Day-neutral	*Phlox paniculata*
Short	Day-neutral	Late rice varieties
Day-neutral	Short	*Chrysanthemum osticum*
Day-neutral	Long	Spinach, wheat
Day-neutral	Day-neutral	Pepper, early rice, buckwheat

Whether many plants, in flowering and fruiting are as closely adjusted to the light period as would seem to be indicated here, may be questioned, for often changes in length of day merely delay flower development. Then there is considerable evidence extant also that the age of the plant determines in a large measure its sensitivity to length of day (Čajlachjan, 1936; Purvis and Gregory, 1937; Borthwick and Parker, 1938; Moshkov, 1939; Miroljubov, 1940). All this seems to suggest the necessity of revision of our conception of photoperiodism.

The period from flower initiation to their full development (anthesis) should receive at least an equal if not greater consideration than the time of floral inception. Flower differentiation does not always lead to their

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macroscopic development, certainly not in equal numbers (MURNEEK, 1939). The histological analysis by BORTHWICK and PARKER (1938) suggests this, and their further studies on the effects of the photoperiod on development of the Biloxi soybean (PARKER and BORTHWICK, 1939) demonstrate that when plants, with initiated floral primordia, were transferred to long, 16-18 hour photoperiods, no flowers opened, and when photoperiods above 13 hours were given no fruit was formed. NIELSEN (1942) found that even 10 cycles of short photoperiods resulted in a high percentage of degenerated microspores in the Biloxi soybean.

In view of these facts, and the thought-provoking statement by GREGORY (1936) that "the problem of photoperiodism may be considered not as concerning conditions leading to flower formation but as concerning failure to flower," it would seem to be desirable that in studies of photoperiodism, as it affects sexual reproduction and metabolism, the whole reproductive cycle should be followed in detail both by observation and histologically. As far as the writer is aware this procedure was started for the first time with the soybean, var. Biloxi (MURNEEK and GOMEZ, 1936) and has subsequently been used successfully by other investigators (HAMNER and BONNER, 1938; BORTHWICK and PARKER, 1938; SNYDER, 1940; MANN, 1940, etc.).

Selection and breeding of plants for adaptability to localities of certain photoperiods has been in progress for a number of years. The testing of species, varieties and strains was started by GARNER and ALLARD (1920) and has been continued by numerous other investigators. Unconsciously growers have been doing it for a very long time, especially in comparative tests of types and varieties of various economic plants. In this connection emphasis should be placed on the importance of conducting selection by exposing plants to near the critical length of day for flower initiation and development, for there will be revealed the greatest degree of variation in time of flowering (ALLARD and ZAUMEYER, 1944).

Phenotypic adaptation is adaptation of the individual, but there is also genotypic adaptation of successive generations. In adaptability to a locality, therefore, not only the environment but also the endogenous rhythm of the selected plants must be taken into account. These do not always coincide. Though we do not know much about the specific mechanism of this "inner rhythm," it probably originated as a result of natural selection of random mutations, but segregation and recombination or other gene mechanisms may be operative (LUBIMENKO, 1939; BÜNNING, 1943). Breeding plants for photoperiodic adaptability has been successful in several instances (MUNERATI, 1931; ABEGG, 1936; OWEN *et al.*, 1940; GOODWIN, 1944, etc.).*

Technique and Application: — The original technique of treating plants for photoperiodism, as used by GARNER and ALLARD and others, was to grow them in any convenient containers and either shorten the natural photoperiod by placing them during part of the day under an opaque cover

* On the hasis of behavior analysis of F_2 plants, obtained from hybridization of Maryland mammoth (short-day) and Java (day-neutral) varieties of tobacco, A. LANG (Special Supplement 3, pp. 175-183) has reached the conclusion that the short-day character in Maryland mammoth tobacco is recessive to the dominant day-neutral character and monofactorial in inheritance. This characteristic response to a short photoperiod is probably the result of quite frequently occurring gene mutations in this and many other races of tobaccos.

of some sort or in a ventilated darkroom, or by extending the photoperiod with electric illumination. This can be done either in the greenhouse throughout the year or outdoors during the growing season. Quite similar procedure has been used by later investigators, excepting for variability in kind of light employed, such as the use of incandescent bulbs, carbon arc, fluorescent tubes, etc.

The intensity of radiant energy given to plants to extend the length of day has varied greatly, but commonly has been more than 100 f.c. As regards photoperiodism, most plants seem to be sensitive to surprisingly weak illumination, occasionally to as low as 0.1 f.c. (WITHROW and BENEDICT, 1936). Light from as large electric lamps as 1000 watts, if too close, may increase excessively the plant's temperature, requiring the interposition of cooling equipment, such as a cell of running water. Details in the lighting procedure were introduced when some part of the plant was exposed to one and another to a different light regime, as in studies of localization of the effect.

STEINBERG (1931) and GARNER (1936) have described and used to some extent for photoperiodism studies elaborate equipment in the form of air-conditioned cabinets, in which plants are grown entirely under electric light, controlled temperature, humidity, air movement, etc.—in other words, an artificial climate. WENT (1943) and LEWIS and WENT (1945) have used air-conditioned greenhouses, with light, temperature and humidity under control. For investigations on the relation of temperature to length of day effects, the greenhouse temperature must be controlled either during the dark or light periods or both (THOMPSON, 1933; ROBERTS and STRUCKMEYER, 1938, 1939; LONG, 1939, BORTHWICK *et al.*, 1943), while for detailed tests on parts of the plant, leaves, stems or growing points have received special chilling either by means of air or water currents (CHROBOCZEK, 1937; BORTHWICK, 1943).

In determination of the photoperiodic responses to light of certain wave lengths, various filters have been employed (WITHROW and WITHROW, 1940; WENT, 1944) but direct spectrographic light has also been tried (PARKER *et al.*, 1945).

Comparatively recently grafting procedures have come into vogue in studies of translocation of the photoperiodic stimulus (MELCHERS, 1937; ČAJLACHJAN, 1937, 1938; HAMNER and BONNER, 1938; HEINZE *et al.*, 1942; STOUT, 1945). Undoubtedly other special techniques will be resorted to in the future for detailed investigations of photoperiodism.

Plants are being given photoperiodic treatments to a considerable extent in modern horticultural practice, especially in connection with greenhouse culture. In the light of our present knowledge it is possible not only to bring introduced species and varieties into flowering or fruiting, but do it at a specific time, either by shortening or lengthening the light period. The timing for specific dates of bloom is a very important floricultural problem, particularly when it is done out of season. This can now be controlled so definitely, by adjusting either the photoperiod or temperature, or both, that recommendations are given by specialists in the field and used in practice (LAURIE and POESCH, 1932; GREENE *et al.*, 1932; POESCH and LAURIE, 1935; POST, 1942).

To shorten the photoperiod, plants are commonly covered with frames of black paper or curtains of black cloth during part of the day, while it may be conveniently lengthened by means of electric illumination of comparatively low intensity. These procedures are quite similar to those used in experimental work.

Tests have shown that plants respond the same whether artificial light is given at the beginning or end of the dark period (Post, 1942). This is in agreement with the early observations by Garner and Allard (1920). A minimum light intensity of 3-5 f.c. seems to be sufficient for most plants, though more uniform results apparently are secured with 10 f.c. or higher illumination. Recent studies have shown that intermittent supplementary flash lighting for ½-1 minute, followed by an equal or a somewhat longer dark period, depending on the kind of plant treated, is equally as satisfactory as continuous illumination and, of course, more economical (Hume, 1940; Snyder, 1940). Quite identical results can be obtained also, so it is said, by interrupting near its middle the dark period with usual lighting for a few minutes only (Parker and Borthwick, 1942).

A desired reaction of plants, whether in delaying or hastening blooming, can be best secured from a reduction or an increase in the length of day when there is previous information on the normal seasonal development and of the reaction of particular plants to specific photoperiods and its relation to temperature and other factors. Moreover, the condition of the plants at the start, and the length of the treatment, determine to a large extent the resultant growth and development.

An interesting application of photoperiodism, conjointly with temperature, on the induction of flowering in embryo-cultured peach seedlings has been reported by Lammerts (1943). If derived from parental varieties with a long chilling requirement, such seedlings form rosettes and go dormant early in the fall. This may be overcome by exposing them to long photoperiods or to continuous light at a relatively high temperature (Minimum 70-75° F.), which lengthens the growth period. With the addition of a brief chilling treatment, this hastens development, resulting in flower production two years after pollination, thus helping to speed up breeding work.

Relation to Temperature: — The modifying effects of temperature on photoperiodism have been known ever since the observations by Garner and Allard, who state (1923, p. 912) that "temperature undoubtedly is the most important environmental factor in relation to the action of the light period on plant growth." When certain varieties of soybeans were grown in greenhouses during winter months (short days) with mean temperatures of 55° F and 72° F, respectively, flowering was markedly hastened by the higher temperature. Subsequent studies with several varieties of soybeans, conducted both outdoors and in the greenhouse, led them to conclude that "under field conditions in Washington, D. C. variations from year to year in date of flowering of both early and late varieties of soybeans, when planted on any particular date, are due chiefly to differences in temperature, while length of day is the primary external factor responsible for the fact that one variety is always relatively early and another late in attaining the reproductive stage" (Garner and Allard, 1930).

In more detailed investigations with soybeans, other field and several horticultural crops, emphasis has been placed to an increasing extent on the importance of temperature in its relationship to the photoperiod (Eaton, 1924; Gilbert, 1926; Plitt, 1932; Thompson, 1933; Purvis, 1934; McKinney and Sando, 1935; Steinberg and Garner, 1936). Flowering and fruiting of late maturing soybeans such as Biloxi for instance, is favored by a combination of short days and warm temperature, of *Rudbeckia bicolor,* by long days and warm temperature, and of sugar beets by long days and cool temperature.

Many winter wheats and other winter cereals are not really typical long-day plants, as regards sexual reproduction, but are short-day → long-day plants and may be considered also low-temperature → high-temperature plants. One of these essential conditions, sometimes both, must be obtained during early stages of plant development in order that flowers be initiated. The other, or both, are necessary for successful sexual reproduction. Typical spring cereals probably are long-day high-temperature plants. While the biennial sugar beet apparently requires both a low temperature and long days, the annual beet long days only for sexual reproduction (Owen *et al.,* 1940; Stout, 1945).

By using a great variety of plants, representing several genera and species, Roberts and Struckmeyer (1938, 1939) have demonstrated that the responses of most of them to the length of day are altered, often strikingly, by the night temperatures only a little above or below those customarily used in greenhouse practice. *Poinsettia,* a commonly considered short-day plant, for example, failed to bloom under this photoperiod when grown at a minimum temperature of 55° F. The long-day *Rudbeckia laciniata* was similarly influenced by temperature in its response to length of day. At a night temperature of 60-65° F and short-day light exposure it remained in a rosette stage of growth, but with the same photoperiod at 55° F. it grew in height and eventually produced flowers.*

From these and similar observations it is quite apparent that the sensitivity of many plants to the duration of light is affected very much by temperature and, contrariwise, the photoperiod influences the responses of plants to temperature. From the results obtained on the effects of temperature and photoperiod on some pea varieties, Kopetz (1943) concludes that both day-length and temperature appear to have a decisive influence on plant development. Under short-day treatment, however, the influence of temperature seemed to be masked by a stronger effect of day length, but under long photoperiods temperature seemed to be the determining factor of development. Responses to the photoperiod and temperature of several native California annuals, studied by Lewis and Went (1945) pointed to the fact that all but two were long-day plants and reactive to the night temperature.

One should be always aware of the fact, in observing responses of

* *Viola hirta* and *V. silvestris,* according to P. Chouard (Comptes Rendus 224: 1523-1525, 1947) produce cleistogamous flowers continuously in a long photoperiod (12-14 hours) if the temperature permits uninterrupted vegetative development (greenhouse culture). When the day length is 8 hours, however, they form chasmogamous flowers, hut only when the plants have been exposed to a period of frost. An annual temperature rhythm, therefore, is necessary for this mode of flowering. The reaction of these two species differs from that of *V. papilionacae* which does not seem to be adjusted to thermoperiodicity.

plants, that the temperature or the photoperiod or both may merely delay flower development, of which there are numerous instances on record and many others would have been observed if the experimental plants had been grown long enough. In analyzing the photoperiodic and temperature reactions of soybeans obtained from different regions, RUDORF and SCHRÖCK (1941) noted that the higher temperatures given only in the early stages of exposure to short-days hastened the beginning of flowering and that this was irrespective of temperature and photoperiodic conditions obtaining afterwards. HEATH (1943) found that both long days and high temperature promoted bulb formation and prevented bolting of onions, but short days inhibited bulb production but allowed bolting, if the temperature was not too high. Day lengths sufficiently long for bulbing at high temperatures will prevent their formation at low temperatures. Planting onions late in the season, when days are sufficiently long, will produce satisfactory bulbs, depending largely on the prevailing temperature. While studying the effects of some environmental factors on floral initiation in *Xanthium pennsylvanicum,* a short-day plant, MANN (1940) found that the temperature during the photoperiod had a pronounced influence on the resultant time of flowering, but as the photoperiod increased in length, the temperature effects diminished. Temperature seems to have a bearing also on the length of the critical dark period required by this plant (LONG, 1939).

Whether the night or the day temperature is most important has not been determined for all species and varieties (THOMPSON, 1944). More or less specific night temperatures are now commonly considered as being desirable for raising ornamentals in greenhouses. Cineraries, cyclamens, chrysanthemums, carnations and snapdragons are usually grown at a night temperature of 45-50° F., roses and begonias at 60° F., and gardenias, orchids and bouwardias above 60° F. (POST, 1942).

In consideration of the accumulated information on the relationship of temperature to photoperiodism, both are now being taken into account in experimental work on the influence of length of day on plant development and either the day or night temperatures, or both, are kept under control (RUDORF and SCHRÖCK, 1941; ÅBERG, 1943; SIVORI and WENT, 1944; LEWIS and WENT, 1945; LOVVORN, 1945).

Of considerable interest in this discussion should be the fact that temperature itself, independently of the photoperiod, may be a potent factor in induction and maintenance of sexual reproduction in plants. KRAŠAN, as early as 1870, had called attention to temperature as a factor in initiation of flowering of many plants and KLEBS (1913) observed that when beet roots were kept during the winter in a warm greenhouse no flowers were produced the following summer, as this biennial plant usually does, while roots stored outdoors flowered and set seed abundantly.

The extensive investigations by THOMPSON and associates (1933, 1939) on vegetables, by POST (1937, 1940) on ornamentals and by others would seem to furnish ample testimony that various plants, though responsive to photoperiod, can be induced to bloom by temperature treatment alone, commonly by "chilling." In some recent studies on the effects of temperature on initiation of flowering in celery, THOMPSON (1945) found that an exposure for as short a period as 2 days at 40-50° F caused floral inception,

though the plants were exposed subsequently to temperature too high (60-70° F) for this process. This was true whether the low temperature treatment was given during the dark or light phase of the 24 hour cycle. But when the plants were kept at 70-80° F, after a cold exposure even up to 32 days, no flowers were developed. This reminds one of so-called devernalization of cereals by high temperature (Purvis and Gregory, 1945).

According to Went (1945), the cultivated tomato, a photoperiodically neutral plant, sets fruit abundantly only when the night temperature is between 15-18° C and the day temperature about 25° C. With lower and higher temperatures at night fruiting is reduced or absent. This diurnal alteration in temperature requirement would seem to be a sort of simulation of photoperiodicity by thermoperiodicity. The conclusion is drawn from these observations that thermoperiodicity in the tomato, and possibly other plants, is due to the predominance of two processes, one during the day and the other at night, of which the one in the dark evidently has a much lower temperature requirement. Temperature probably acts directly on the terminal meristematic regions, instead of indirectly through the foliage as the receptive organ, as in photoperiodism (Curtis and Chang, 1930; Chroboczek, 1934).

Photoperiodic Induction: — In their studies of the influence of various photoperiods on reproduction of soybeans Garner and Allard (1923) observed that an exposure to 10 short days was all that is required to bring about flower formation, which was continued when the plants thereafter received long-day exposures. Since then numerous investigators have observed in a variety of plants that an initial treatment to a light period conducive to sexual reproduction will result in flower and fruit development, though often to various extents, irrespective of the length of day to which the plants are subjected afterwards (Čajlachjan, 1933, 1935; Eghis, 1928; Lubimenko and Ščeglova, 1927, 1931, 1933; Purvis, 1934; Psarev, 1930*b*; Rudorf, 1935). This seems to be true of both short- and long-day groups. The effect has been named "photoperiodic induction" or "photoperiodic after-effect." Recognition of this phenomenon has been of great value in detailed studies of photoperiodism in many plants, especially in analysis of the nature of the photoperiodic reaction.

Plants seem to vary as to their sensitivity to photoperiodic induction, depending not only on the genus and species but also variety and even strain. Thus, for instance, *Baeria chrysostoma,* a relatively short season annual, apparently requires at least 5 photoperiods for flower induction (Severi and Went, 1944), while for the Biloxi soybean and for *Xanthium,* with much longer life spans, two and one photoperiods, respectively, apparently are sufficient to differentiate floral primordia (Borthwick and Parker, 1938*a;* Naylor, 1941). It is stated, however, that the longer the treatment the sooner the blossoms developed in Biloxi, and that in *Xanthium* a single photoperiodic cycle required a comparatively long time (64 days) for flowers to mature, whereas 4-8 such cycles led to flower development in a more normal time and under continuous induction, in 13 days. Moreover, with increasing number of photoperiodic cycles given there was a proportional increase in number of flowers initiated (Hamner, 1940).

Not only the photo but also the dark period seems to be essential as re-

gards photoperiodic induction of short-day plants. Long (1939) found that at least 3 long dark periods must be given consecutively to initiate flowers in Biloxi soybeans and that variations in temperature affect considerably the length of the critical dark period. In *Xanthium,* likewise, the response is largely a reaction to the dark period (Hamner and Bonner, 1938; Mann, 1940; Hamner, 1940). While in both the light and dark phases of the inductive cycle, temperature and probably other environmental factors may modify or even inhibit the response of plants to induction, with increasing number of photoperiods the temperature effect usually becomes less noticeable. Moreover, there is the possibility that a certain length of night, like that of day, may be conducive to initiation of floral primordia, while a different dark period may be better for further development of flowers or for their function (Purvis, 1934).

Recent detailed investigations of the relationship of the light and dark periods of the inductive cycles, previously referred to, have been summarized critically by Hamner (1942, 1944). The conclusion is drawn that in short-day plants photoperiodic induction consists most probably of an inductive cycle requiring photoperiods of a minimum duration and intensity and dark periods of minimum duration. In agreement with this conception appear to be the findings of Moshkov (1939, 1940) and Čajlachjan (1941), who, in their studies on several short-day plants, also observed that an alternation of light and darkness was a prerequisite for inception of flowering in this group. In *Perilla ocymoides,* for example, 9 hours of darkness and 9 hours of light was found the minimum diurnal requirement for flowering. Rasumov's (1941) experimental evidence has led him to believe that in short-day plants initiation and growth of reproductive organs takes place during the dark period but development in long-day plants occurs chiefly in light, which probably do not require for this function an alternation in light and dark periods. Several years previously to the above investigations Lysenko (1931, 1932) suggested that long-day plants require light for completion of sexual reproduction (his second or light phase of development) while short-day plants require darkness for it. But since such plants cannot exist for any length of time in continuous darkness because of absence of photosynthesis, alternating periods of light and darkness are essential.

Present information does not seem to indicate that long-day plants require for flower-induction a cyclic change of light and dark periods, for they have been made to bloom in continuous light. Hamner (1944) is of the opinion that in nature flowering in both groups of plants is determined by the length of night: "In short-day plants flowering seems to be stimulated by long dark periods while in long-day plants flowering tends to be inhibited by long dark periods." This is in conformity with Blackman's (1936) suggestion that the length of the night was chiefly responsible for photoperiodic induction of flowering.

Light intensity, to some extent, is a factor in this process. In artificial light Biloxi soybeans were found to initiate flowers at intensities of 100 f.c. but not below it (Borthwick and Parker, 1938*b*). When daylight was extended with Mazda light, initiation did occur if the supplementary light was less than 0.5 f.c. Biloxi soybeans did not form flowers when kept during the short (8 hour) photoperiods at light intensities of

10-20 f.c., though light of high intensity (natural daylight) was given for 1 hour of the 8 hour period. But with 2 or more hours of intense light during the photoperiod, increasingly more initiation of reproductive structures was obtained (PARKER and BORTHWICK, 1941). WITHROW and BENEDICT (1936) could see little difference in response of several greenhouse annuals when the day length was extended with artificial light at intensities from 10 to 100 f.c. Definite photoperiodic effects were secured with 0.3 f.c. and the China aster reacted even to light of 0.1 f.c. RASUMOV (1935) observed that oats and millet, obtained from various localities, responded differently during their photoperiods to light intensities.*

Studies of the effects of light of various wave lengths on photoperiodic induction so far seem to have advanced very little our knowledge of the mechanism of inception of the photoperiodic reaction, though this undoubtedly is one of the most crucial phases of the phenomenon. RASUMOV (1933) and KATUNSKIJ (1937) found that red light had a similar effect to white light in flower initiation, but green, blue and violet radiations were like darkness in this respect. This is but a confirmation of KLEBS' observation that red light is most effective in promotion of sexual reproduction. It was confirmed again by WITHROW and associates in 1936 and 1940. SCHAPPELLE (1936), however, claimed that red and blue radiations were more or less equally effective for spinach, radish, cosmos, lettuce and China aster.

In more detailed studies of the influence of wave lengths of artificial light used to lengthen the daylight period (WITHROW and BENEDICT, 1936) obtained from orange and red light (650 + mμ) the greatest photoperiodic effect in pansy, stock and aster plants and little response from other wave lengths. They conclude that the photoperiodic perception mechanism probably has a maximum intensity at 650-720 mμ of radiation. For *Baeria chrysostoma* all wave lengths, excepting green, were found effective in induction of flowering. Light of different colors was obtained by passing radiation from 1000-watt incandescent lamps through appropriate glass filters (SIVORI and WENT, 1944).

Mechanism of Photoperiodism: — This would seem to be a formidable heading, for there is little more than circumstantial evidence, fragmentary at that, on the possible steps involved in the reaction of plants to the photoperiod. Perhaps we can allow it to stand, since it, in a general way, covers various and some very important phases of investigational work on the subject.

The leaves of a plant are the organs through which the photoperiodic stimulus is received. Light, as regards duration and to some extent intensity, is the activating agent. The first reaction, unknown at present, probably is of a photochemical nature. There is ample evidence extant that, as a result of the photoperiod, a substance of a catalytic character, of the nature of a "hormone," is formed which is responsible directly or indirectly, for the induction of floral primordia. This concept is based on a large body of experimental records, first presented by PSAREV, MOSHKOV

* According to N. J. SCULLY and W. E. DOMINGO (Bot. Gaz. 108: 556-570, 1947) both duration of photoperiod and light intensity influence the formation of floral primordia in certain varieties of the castor bean, a long-day plant. They differ, therefore, from *Xanthium* or Biloxi soyheans, which are not very sensitive to differences in total radiant energy but highly sensitive to differences in day length. Results with hybrids were inconclusive.

and ČAJLACHJAN and subsequently by other investigators. ČAJLACHJAN (1937) has tentatively named this substance "florigen." It is formed in the leaves and thence transported to other parts of the plant, primarily to certain terminal meristematic regions of the stem where flowers are initiated. This concept is but a resurgence of the idea conceived by SACHS (1863-1866) that flower producing substances ("Blühstoffe") are formed in the leaves and translocated to terminal meristematic regions where flower formation occurs.

Though perhaps other portions of the plant may react to some extent to the photoperiodic stimulus, apparently the fully developed new leaves are the chief loci of perception. The young developing and the old ones may even inhibit the photoperiodic reaction of the mature leaves, either by diluting or destroying the substance produced (HAMNER and BONNER, 1938; NAYLOR 1941). But ČAJLACHJAN (1937) and STOUT (1945) state that the vegetative shoots do not seem to produce a substance that is antagonistic to sexual reproduction. The hormone seems to be stored to some extent in the leaves. When taken from photoperiodically induced plants and grafted on vegetative ones, they continue to supply the hormone (LONG, 1939), although there is evidence to the contrary (MOSHKOV, 1941). Light intensity and temperature, as was pointed out previously, have an important bearing on hormone formation in the leaves.

The production of the photoperiodic impulse in the leaves probably stands in no direct relationship to photosynthesis (POTAPENKO, 1944) since (*a*) it can take place in very weak light which does not permit much photosynthesis and during which respiration certainly is in excess of carbon assimilation and (*b*) reduction of the light period in short-day plants, which would seem to curtail the amount of carbon assimilation, leads to initiation of reproduction. Moreover, ČAJLACHJAN (1941) has shown the photoperiodism takes place whether the plants are green or chlorotic. On the other hand there is evidence more or less to the contrary. By controlling photosynthesis, either through limitation of CO_2 supply or duration of light intensity, initiation of floral primordia was limited in the Biloxi soybean (PARKER and BORTHWICK, 1941; HARDER and WITSCH, 1941). Suggestive of a connection between photosynthesis and photoperiodism are also the results obtained in suppression of floral initiation by interruption of the dark period with spectral light. It showed two regions of maximal efficiency (suppression), one in the red, the other in blue light, thus indicating a possible association, negative though it be, with chloroplast pigments and photosynthetic utilization of carbon dioxide (PARKER *et al.*, 1945).

WITHROW and WITHROW (1944) have concluded, from their work on intermittent irradiation of several kinds of plants, that the kinetics of the photoperiodic reaction is based on two relationships which appear to limit the photochemical reaction: *a*) "The relatively slow rate of the non-photochemical reaction which forms the substance to be photoactivated and *b*) the relatively low equilibrium concentration which this substance attains during long periods of darkness." This suggests some possible limitations in two hypothetical reactions but does not indicate their essential character.

In order to account for the response of Biloxi soybean and *Xanthium* plants to both the photo- and the dark-periods of the alternating cycles

necessary for photoperiodic induction, HAMNER (1942, 1944) has presented what he calls "a simple hypothesis," for the support of which a certain amount of experimental data have been secured with these plants. Therefore, it seems to be based on inferences which have already the weight of some evidence in its favor. To quote HAMNER: "It appears that determinative reactions take place during both the light and dark phases of the cycle and also that there is an interaction among them. For convenience the changes or conditions which arise owing to exposure to light may be designated as A, those owing to darkness as B, and the possible summation or resultant changes related to A and B may be referred to as C. Thus, an interaction between A and B results in C. Such a postulation necessarily implies a carry-over of the effects produced during the photoperiod into a subsequent dark period, or a carry-over of the effects produced during a dark period into a subsequent photoperiod, since such must be the case in order for the interaction to take place. It is assumed that through the medium of C the observable effects, such as differentiation of floral primordia, flower development, and the like are manifested."

While the symbols A, B and C have been used for convenience to express possible steps in the photoperiodic responses of Biloxi and *Xanthium* plants, HAMNER emphasizes that they may represent a whole series of interlocked reactions involving many substances. The experimental data would seem to suggest that A is a relatively stable substance, which is formed during exposure to light and evidently depleted during the subsequent dark period because of reaction with B to form C. During the exposure to darkness B probably increases in amount till a threshold value is reached when an interaction with A takes place. Whatever its nature, B apparently is destroyed by as brief an exposure to light as 1 minute. C appears to be relatively unstable also for the amount formed during one photoperiodic cycle is not usually carried over to another, if an intervening non-photoperiodic cycle is set between them. The action of C evidently is increased by light intensity obtaining after the photoinductive cycle. It should be emphasized that there is no confirmation of this hypothetical scheme.

Since long-day plants do not seem to require an exposure to darkness, the above hypothesis cannot be applied to them. Neither is it suitable for the so-called "neutral" plants nor applicable to the action of the light period on modification of vegetative organs and other photoperiodic effects.

The chemical nature of the flowering hormone(s) is unknown. Several investigators have shown, by grafting experiments, that it is the same whether formed by the action of long or short photoperiods. It has been effectively transmitted from annuals to biennials and interchangeably from short to long or neutral plants and vice versa, in various combinations (KUIJPER and WIERSUM, 1936; MOSHKOV, 1937; MELCHERS, 1937, 1938; STOUT, 1945).

The idea that, instead of a special hormone, plant growth substances, specifically the auxins, in some way may be responsible for initiation of the flowering state has been proposed by some investigators of whom the main representative is CHOLODNY (1939). The present evidence seems to be largely against it. But some indirect support to this assumption may be presented from the interesting experiments on flower induction in the

pineapple by means of ethylene and acetylene and synthetic growth substances, naphthaleneacetic and 2,4-dichlorophenoxyacetic acids (OVERBEEK, 1945). Then, too, these and related chemicals have been widely used to stimulate fruit setting and size in tomatoes, beans and a few other plants. There is some evidence that the growth substances increase the auxin content of plants and that ethylene and acetylene, by acting on the mature leaves, may release a flower forming substance (TRAUB *et al.*, 1939).

Tests have indicated that the flowering hormone is not identical with the following substances: Vitamins B_1, B_2, B_6, ascorbic acid, nicotinic acid, pantothenic acid, or theelol, inositol or indoleacetic acid (HAMNER and BONNER, 1938).

Judging from the results frequently obtained, the production of florigen has certain quantitative aspects. With increasing amount of foliage, light intensity, number of photoperiods and change in temperature more of it or less may be formed, as has been pointed out already. When there is a lack of sufficient quantity of the hormone, flower production may be suppressed or their development may be incomplete (MURNEEK, 1939). Morphological and histological variations of flowers because of insufficient photoperiodic dosages or correlated disturbances, leading in extreme cases to their anomalous development, the formation of so-called "vegetative" flowers, has been described by BIDDULPH (1935), MURNEEK (1936-1940), GREULACH (1942) and HARDER *et al.* (1942).

HARDER undertook an extensive study of the effects of a reduced flower hormone supply on the formation of inflorescences of *Kalanchoe blossfeldiana* by the following experimental means: *a*) Limited number of effective photoperiods (short days); *b*) the use of intermediate photoperiods; *c*) lowering of temperature at night; *d*) interference with transport of hormone by cutting of midribs of donor leaves and *e*) variations in distance of transport of hormone. The results showed that all the above procedures, properly executed, reduced the formation of flowers and changed to various degrees inflorescences into vegetative shoots. He makes the interesting observation that the vegetative organs near inflorescences, because of the latter's reduction in size or complete absence, were changed, and expresses the belief that these vegetative organs are even better indicators than the flowers themselves, of the amount of hormone present.*

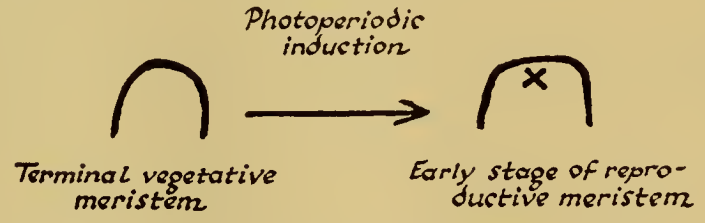
The transport of the hormone from the leaves to the apical meristems and elsewhere seems to be of the nature of diffusion, involving living cells. Hence the rate of transfer both through the leaf petiole and the stem is comparatively slow. When the main vein of a leaf is cut, there does not appear to be an interference in hormone movement from the leaf to the stem. It does not seem to be translocated either through the xylem tissue

* GERTRUD MEYER (Biol. Zentrbl. 66: 1-20, 1947) has demonstrated that in *Sedum kamtschaticum* an exposure of as small a leaflet as ½ cm^2 to a long photoperiod will affect to some extent the development of other parts of the same plant kept in a short photoperiod. Hence in *Sedum* (long-day plant) a relatively small leaf surface area has the same or similar effect on flower hormone production and/or transfer as a much larger leaf area in *Kalanchoe* (short-day plant). There does not seem to be enough evidence for the special catalytic substance ("Metaplasin") assumed to be produced by the photoperiod, and to function in modifying the vegetative parts of the plant, which is postulated by HARDER *et al.*, and agreed with by MEYER (1947). The morphogenetic effects on vegetative organs are most likely the results of photoperiodically induced sexual reproduction (MURNEEK, 1936, 1939, 1940) (*cf.* p. 90).

or through dead petioles. When the bark is removed, there is no transfer of the hormone (ČAJLACHJAN, 1938, 1940, 1941; HAMNER and BONNER, 1938; BORTHWICK *et al.*, 1941; WITHROW and WITHROW, 1943; STOUT, 1945).

The hormone moves up and down the stem with almost equal facility, though the upward transport is the more common direction (HEINZE *et al.*, 1942). It may be stored to some extent in the stem and probably other parts of the plant. Some believe that the hormone can be transferred through an inert partition such as lens paper, inserted at the union between the two graft symbionts (HAMNER and BONNER, 1938) though more recent findings seem to show that its translocation between donor and receptor plants is possible only when there is established a direct union (MOSHKOV, 1939; WITHROW and WITHROW, 1943).

The hormone moves to the terminal meristems where in some unknown way it affects the apical cells changing their activity from production of vegetative tissues to inception of floral primordia. Not all of the meristems are in the same stage of development at any particular time of induction, or perhaps do not get the same dosage of the stimulant or else are not equally susceptible to it. Those nearest to the photoperiodically most sensitive leaves may perchance receive the hormone sooner or in larger amounts than the more distant ones, for when buds nearest to the functional leaves are removed other buds seem to get more of the catalyst. BORTHWICK and PARKER (1938) have shown that the first microscopically visible response in the Biloxi soybean, as a result of exposure of the whole plant to 5 or 6 short days, was in the buds located in axils of leaf primordia that were fourth or fifth from the tip of the main stem. HARDER *et al.* (1942) think that in meristematic regions the hormone is distributed throughout the tissue, but even here there may occur a one-sided effect. The production of flowers with only partial expression of the reproductive organs and associated tissues, already referred to, would seem to suggest an incomplete supply of the hormone to meristems from which they arose or else interference at some later stage in flower development.



One of the crucial aspects of the photoperiodic induction of floral primordia unquestionably is the first changes in the vegetative meristems, more accurately the retardation in multiplication of the apical cells. It is well known that the first microscopically observable alteration at the rounded tip of the meristem, that changes toward the formation of reproductive tissues, is the formation of a plateau. The meristematic cells are inhibited at X. It would seem to be very desirable to conduct detailed cytological and possibly microchemical studies of the meristem during the earliest changes toward reproduction as effected by the photoperiod and

possibly other environmental factors (SINNOTT, 1938). And if we consider GREGORY's idea that the problem of photoperiodism in plants is not really concerned with factors that determine flower formation but those that lead to failure of flowering, then other later phases of development of floral organs, as influenced by the photoperiod, must likewise be taken into detailed consideration.

One should recognize the following stages in flower inception, development and function (MURNEEK, 1937, 1939):

a) Terminal meristems or determined loci where the floral hormone is received and condition of "ripeness to flower" established physiologically. Usually there are far more such meristematic points than there is available hormone or other indispensable substances. Some of them, perforce, cannot initiate reproductive tissues. This is the first elimination of certain meristems as flower producers.

b) With a large number of meristems made "ripe to flower" and having formed floral primordia, it is very probable that many of them are eliminated early because of lack of supply of building material of one sort or another. Organic nitrogen compounds most likely play an important role here. Possibly certain catalytic substances or other hormones, necessary for the early development of floral organs, should be considered also as factors.

c) Further elimination of a large proportion of the developing flowers undoubtedly occurs because of competition for available food supply during their growth. Far more floral primordia are usually formed than can possibly develop into functional flowers. The greater the limitation in reserve food supply or synthesis of organic substances (lack of light or extreme temperature) the fewer flowers will be brought to completion (MURNEEK, 1926).

d) Not all flowers that reach anthesis are able to function normally, *i.e.* to form gametes and participate successfully in fertilization. There may be various reasons for this condition. Some flowers, though appearing normal on casual observation, are abnormal in many essential morphological structures, such as incomplete development of stamens or ovaries or the micro- or macro-gametophytes. It is a common knowledge that plants often produce an enormous number of flowers of which only a small proportion participate in fertilization (LOEHWING, 1938; NIELSEN, 1942).

In the delicate balance between vegetation and reproduction the growth rate and photoperiodic or other inhibition of the main axis and lateral branches should be taken into account (MURNEEK, 1936, 1939, 1940). Stem elongation is promptly retarded in the Biloxi soybean, *Rudbeckia bicolor, R. hirta* and many other plants by exposure to a short photoperiod (MURNEEK, 1936, 1940; GREULACH, 1942). In the soybean, var. Biloxi, this treatment probably effects independently induction of reproduction and inhibition of vegetative growth, although it is possible that a special inhibiting substance may be produced by the floral primordia. The writer found that growth of the main axis of *R. bicolor,* a long-day plant, cannot be induced but only maintained on a long photoperiod. Growth in height stopped promptly when the plants were moved from long- to short-day exposures. It was found possible to combine photoperiodic induction and photoperiodic inhibition in various ways in *R. bicolor* plants by exposing them to certain number of long and short light periods. Size and form of the vegetative parts and amount and character of flower development thereby was changed.* Stem elongation has been found to be inhibited by

* Another example is reported by J. C. SEN GUPTA and S. K. PAYNE (Nature 100: 510, 1947) who show that leaf heteromorphism in *Sesamum orientale* evidently is related to the photoperiod. With increasing length of day, from 10 to 16 hours, there was a reduction in the number of linear lanceolate leaves produced and an increase in number of ovate entire and ovate serrate leaves. Moreover, plants that received a 14-hour or a longer photoperiod produced larger and more variable leaf forms than plants given a 10-hour photoperiod.

long days in cucumber and by short days in some tobaccos, both of which apparently are day neutral plants (Danielson, 1944; Dennison, 1945). Photoperiodic inhibition has an important bearing on nutrition and metabolism of plants and thus on flower development and performance.

Conclusion: — The discovery of photoperiodism and the subsequent disclosure of the effects of temperature on plants have emphasized forcefully that the genetically determined rhythm of development can be modified strikingly by the environment. It has advanced our knowledge on certain aspects of latitudinal and seasonal adaptation of a considerable number of species and varieties.

The present commonly used classification of plants into short-day, long-day and neutral types, however, is not acceptable any more, in consideration of recent investigations. In nature probably no plant throughout its life is adapted strictly to one kind of photoperiod, excepting those growing in equatorial regions, but many plants will tolerate to a considerable extent a uniform length of day, as when grown under such conditions for experimental purposes. Most likely a specific length of day or night is most conducive to one phase of sexual reproduction of particular plants and another or others to succeeding phases. There is urgent need for more detailed studies of the effects of the light period not only on initiation of the sexual state but especially on flower development and fruit and seed production.

We may well expect to gain a clearer understanding of the often very close adaptability of plants to their ecological environments from further studies on the reciprocal influences between photoperiodism and temperature and possibly other environmental factors. The information thus gained should be of increasingly greater importance in cultural practices of many economic species and varieties. Application of photoperiodism and control of night temperature has already been of considerable practical value in connection with greenhouse culture of certain flowers and vegetables and in the breeding and selection of a large variety of field and other crop plants.

Despite the extensive investigational work that has been conducted on the problem, exact information on the mechanism of photoperiodism is still lacking. It is fairly certain, however, that, as a result of the photoperiodic stimulus, a catalytic substance of hormone-like nature is formed in the leaves, whence it moves to the terminal meristems resulting in initiation of floral primordia. If the inductive action, either during the light or dark periods of the diurnal cycle, is of a photochemical nature and in a way analogous to photosynthesis then detailed physico-chemical studies are in order and many difficulties may be encountered in analysis of the problem. Considerable advance in our understanding of photoperiodism would be gained if the flower inducing hormone ("florigen"), unstable as it may be, could be isolated in pure form and its chemical constitution determined. This would seem to be the first crucial problem for solution.

The function of the photoperiodically formed hormone in altering the activity of terminal meristematic cells, from production of vegetative to reproductive tissues, has received practically no attention so far, beyond some general histological observations. Cytological and chemical studies of

meristems, as altered by the photoperiod, would seem to be highly desirable. Here we deal with the second most crucial problem of photoperiodism—the induction of sexual reproduction. Perhaps a less complicated approach to solution of the mechanism of floral induction would be by the use of temperature as the external modifying factor, for it appears to act more directly on the terminal tissues.

While these and other fundamental questions should, and eventually will, be answered in studies of photoperiodism, further advances should be made in the application of the phenomenon to various phases of plant culture and related problems.

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HORMONES IN RELATION TO VERNALIZATION AND PHOTOPERIODISM

by

KARL C. HAMNER

United States Plant, Soil and Nutrition Laboratory, Ithaca, N. Y.

In recent years a great many investigations have been concerned with the internal changes in plants which lead to the differentiation of flower primordia and the development of flowers. Much interest has centered in the earliest changes which take place in the plant which mark the initial transition from the vegetative to the flowering condition. This present discussion will deal primarily with these early changes and with several theories which postulate the sequence of events leading to the differentiation of flower primordia. No attempt will be made to give an adequate review of the literature since it has been carefully covered in other chapters. Selected references will be made to illustrate particular points.

Many years ago, SACHS postulated the existence of "organ-forming substances" in plants. He produced no definite evidence for the existence of flower-forming substances. GARNER and ALLARD (12) working with *Cosmos sulphureous,* a typical short-day plant, demonstrated the localization of the flowering responses to photoperiod when one part of the plant was exposed to short day and the other part to long day. They demonstrated that a portion of the plant exposed to continuous darkness exhibited some response when an adjacent portion of the plant was exposed to short day, indicating some transmission of the short-day stimulus to the darkened portion of the plant. KNOTT (19) working with spinach, a long-day plant, found that exposure of the bud to long-day conditions did not induce flowering if the leaves were exposed to short day. On the other hand, exposure of the buds to short day did not inhibit flowering if the leaves were exposed to long day. KNOTT concludes, "the part played by the foliage of spinach in hastening the response to a photoperiod favorable to reproductive growth may be in the production of some substance, or stimulus, which is transported to the growing point." Most of the credit for the recognition of the green leaves as the organs for the perception of the photoperiodic stimulus, however, must go to two Soviet botanists, ČAĬLAHJAN and MOŠKOV, both of whom, apparently working independently, performed conclusive experiments which indicated that the green leaves first perceive the photoperiodical stimulus which is then transmitted to the growing point. Since then, many investigators have obtained similar results in photoperiodic studies.

Perception of the Photoperiodic Stimulus: — There can be little question that the green leaves are the organs which perceive the photoperiodic stimulus. This has been shown for both long-day and short-day plants (5, 10, 17, 19, 25). The young expanding leaves seem to be in-

sensitive, while the sensitivity of the fully-expanded foliage leaves seems to depend somewhat on the age of the leaf, the youngest being the most sensitive, and the oldest, mature leaves being relatively insensitive (2, 13, 26, 32, 34, 37). Individual plants become more sensitive to photoperiodic treatment as they grow older, but it may be that this increase in sensitivity is related to the fact that older plants have a greater number of foliage leaves to receive the stimulus.

In short-day plants, of course, the leaves respond to exposure to short-day conditions. Evidence is accumulating that an effective short day must contain a photoperiod of a certain minimum intensity and duration of illumination followed by a period of complete darkness of a certain minimum duration. HAMNER (15) has concluded that an effective short day for *Xanthium pennsylvanicum* must include a photoperiod of approximately 30 minutes or more (the length required is dependent on light intensity) followed by a dark period of more than 8½ hours. The above sequence is not reversible with *Xanthium;* the photoperiod must precede the dark period. With Biloxi soybean (1, 14, 15) an effective short day also must include a photoperiod of over a certain minimum intensity and duration of illumination (the minimum length is about one hour and the maximum length is about 20 hours) and a period of complete darkness of more than 10¼ hours. Two or more (usually three or more) of these short days must occur in direct succession if flowering is to result. MOŠKOV (28) with *Perilla ocymoides* concludes that this plant in order to be stimulated to flower must have uninterrupted dark periods of more than 8 hours and must have light periods of more than three hours. He (29) noted that short-day plants must be exposed to a cyclic alternation of light and darkness although he emphasized the importance of the length of the dark period. ČAĬLAHJAN (7) also concludes that short-day plants respond to a definite cyclic alternation of light and darkness. Until evidence to the contrary is forthcoming, it seems desirable at this time to conclude that the specific length and character of both the photoperiod and the dark period determine the results of photoperiodic induction in all short-day plants, and it appears that determinative reactions take place during both phases of the cycle and also that there is an interaction among them (14).

Long-day plants seem to have no requirements with respect to darkness; the initiation of floral primordia takes place in continuous light as well as in the long day (14, 33). A certain minimum intensity of illumination is apparently necessary in order to stimulate flowering, but if the plant is illuminated continuously, it will flower provided it is intermittently exposed to fairly intense light. NAYLOR (33) has shown that continuous illumination does not stimulate flowering in beet unless the illumination intensity is above 700 foot candles. With dill continuous light increased in effectiveness with increasing intensities up to 300 foot candles. Either of these plants will flower if exposed to natural light during the day and to low intensities of light (less than 5 foot candles) at night. It may be concluded that the only effect which dark periods have on long-day plants is to inhibit or delay flowering.

It is of interest to compare the responses of long-day with short-day plants with respect to the influence of darkness. With long-day plants, a

long, dark period seems to inhibit flowering while with short-day plants, a long, dark period seems to stimulate flowering. In either case, if the dark period is interrupted with a short period of illumination, it is non-effective; in long-day plants, it does not inhibit flowering and with short-day plants, it does not stimulate flowering. The dark period may also be rendered ineffective by very low intensities of illumination. In both plants rather high intensities of illumination are required for the stimulation of flowering. While it is true that certain long-day plants seem to be stimulated to flower by the use of low intensities of illumination at night, it seems apparent that this illumination has merely served to shorten the dark periods.

With short-day plants the changes which occur during the dark period and which lead to initiation of flowers should receive more careful study. With *Xanthium,* for example, dark periods of 8½ hours duration are ineffective in stimulating flowering whereas dark periods of 9½ hours are almost as effective as dark periods considerably longer. It would appear, therefore, that changes occur in the leaves after a period of 8½ hours of darkness which result in the production of a stimulus for flowering. Whatever these changes are, in some short-day plants they seem to be of a rather permanent or irreversible nature (this is indicated in the work with *Xanthium pennsylvanicum* and *Perilla ocymoides*). Such chemical investigations as have been made to date have not given a clear indication as to just what these changes are. Apparently during the entire dark period a progressive change is taking place, and this change passes a certain critical point after a very definite length of time. Whatever this change is, it is dependent upon a previous exposure to bright light and the complete absence of light while the actual changes are taking place.

Transmission of the Photoperiodic Stimulus: — The evidence to date indicates that the stimulus is transmitted from the leaf to the stem rather slowly. In *Xanthium* (16), one short day is sufficient to cause the initiation of flowers. If plants receive two short days and are then defoliated, no flowers result. On the other hand, if a small portion of a mature leaf remains attached to the plant, flowering will result. Thus, the stimulus from only a small portion of one leaf is sufficient to cause flowering but not enough stimulus is received from all of the leaves during the first two days of treatment. ČAĬLAHJAN (8) has also concluded that the transfer of the stimulus is slow. One of his arguments for a special flower hormone is based upon his conclusion that the transmission of the stimulus is much slower than the translocation of organic nutrients and growth hormones. Both MOŠKOV (27) and ČAĬLAHJAN (6, 8) conclude that the transfer of the flower-producing substances from the leaves is through living cells. Cooling the petioles (3, 8) greatly reduces or completely stops the transmission of the stimulus also indicating its passage through living cells.

The leaves of some short-day plants apparently continue to supply a stimulus even after the short-day treatment has been discontinued, while with other plants such is not the case. ČAĬLAHJAN (6) with *Perilla* found that large leaves of a plant growing under short-day conditions would induce flowering in a plant continuously exposed to long day when grafted

to it, even though the grafted leaf was placed on long day. Long (22) obtained similar results with *Xanthium*. Čaĭlahjan concluded that the flower hormone accumulated in the leaves of plants exposed to short day and that it was used up in flower bud and flower formation. Hamner and Bonner (16) obtained evidence with *Xanthium* that the continuation of the supply of the stimulus subsequent to a short-day treatment was not due to simple storage of the stimulus during actual exposure to short day but to a continuing generation of the stimulus after short-day treatment was discontinued. Moškov (31) with *Perilla* reaches similar conclusions. Other short-day plants do not seem to continue to supply the stimulus after the short-day treatment has been discontinued. With Biloxi soybeans, Long (22) found that two periods of flowering would result after exposure to two short-day induction treatments occurring about two weeks apart. Botvinovskii (4) obtained similar results with hemp. Thus, a given induction treatment resulted in a certain flowering response and the effect then disappeared.

There is some evidence that the stimulus for flower initiation is used up in the actual process of flower formation and floral development. Hamner and Bonner (16) with two-branched *Xanthium* plants found that the stimulus was received with greater force by the receptor branch (maintained on long day) when all buds of the donor branch (exposed to short day) were removed. It would be of interest to determine whether or not the stimulus would be stored provided there were no buds available to use it up.

The transmission of the stimulus longitudinally through a stem of a short-day plant from a leaf exposed to short day to an actively growing bud is in some way inhibited or partially inhibited by the presence on the stem of mature leaves exposed to long day. Čaĭlahjan and Jarkovaja (9) with *Perilla* found that the removal of such leaves increased the transfer. Hamner and Bonner (16) with *Xanthium* demonstrated that the receptor branch of a two-branched plant, one branch on long day and the other branch on short day, did not flower provided the young leaves were removed and the older, mature leaves remained attached to the receptor branch. With no defoliation or with complete defoliation, the receptor branch flowered. Thus, there were indications that young, developing leaves exert a promotive effect on the transmission of the stimulus which more than counterbalances the inhibitory effect of mature leaves. Borthwick and Parker (1) with two-branched Biloxi soybeans, one branch on long day and the other branch on short day, found that the receptor branch initiated flowers provided its leaves were removed. Heinze, *et al.*, (18) with Biloxi soybeans found that defoliation of a receptor plant of graft-partners increased the response of the receptor. Moškov (30) found that the receptor components of grafted plants responded more satisfactorily if the leaves were placed in complete darkness rather than in long day.

The stimulus is transferred readily across a graft-union. Moškov (25), in his early work from which he first concluded that there was transfer of a stimulus, used two varieties of tobacco, Maryland Mammoth and Sampson. The Maryland Mammoth tobacco is a typical short-day plant,

while the Sampson variety seems to be indeterminate according to GARNER and ALLARD's classification. When both are grown under long-day conditions, the former remains vegetative while the latter produces flowers. The experiments were conducted under continuous illumination, and various types of grafts were made when the plants were at an age at which the Sampson variety was ready to initiate flower buds. Decapitated plants of Maryland Mammoth tobacco were partially defoliated, and scions of either the Sampson or Maryland Mammoth variety grafted to them. Under these conditions, the stock soon produced lateral branches, and these flowered provided the scion was of the Sampson variety and was not defoliated. The stocks did not flower when Maryland Mammoth scions were used. KUIJPER and WIERSUM (20) at about the same time obtained analogous results with soybeans. Since that time many investigators have found it possible to stimulate short-day plants to flower under long-day conditions by grafting to them other plants of the same variety which have been induced to flower by exposure to short day or by grafting to them other varieties or species which will flower in spite of long-day conditions. Most of the grafting experiments have been carried out using short-day plants growing under long-day conditions as the test object and receptor.

MOŠKOV (26) obtained transfer of the stimulus from scions even though the graft union between stock and scion was notably weak. HAMNER and BONNER (16) obtained transmission of the stimulus across what they called "a diffusion contact." They separated the injured surfaces of *Xanthium* plants with lens paper and obtained transfer of the stimulus from a plant treated with short day to the receptor plant maintained on long day. They found no evidence of tissue contact between the injured surfaces of the two plants and assumed that only substances capable of diffusion would have been transferred from one plant to the other. WITHROW (38) repeated these experiments and found that in those cases where transmission of the stimulus occurred cells had grown through the lens paper from one plant to another although admittedly the union between the two plants was very slight.

Vernalization: — A detailed discussion of vernalization has been given in another chapter. For purposes of discussion here, vernalization will be considered to involve the treatment of certain plants with low temperature in order to induce subsequent flowering. Many plants fail to flower unless exposed to a certain period of low temperature either in the seedling stage or after they have developed a number of foliage leaves.

There is a little evidence that hormones may be involved in the vernalization process. MELCHERS (23, 24) induced the biennial form of *Hyoscyamus niger* to flower without a cold treatment by grafting to it the flowering plants of *Hyoscyamus albus, Petunia hybrida,* and *Nicotiana tabacum.* These results indicate that this particular plant, which is ordinarily assumed to require vernalization, may be induced to flower as the result of a stimulus received from other flowering plants without the necessity of vernalization treatment. There is little additional evidence with other plants of this nature.

PURVIS (36) has shown that excised embryos of rye grown on a culture medium may undergo vernalization. There is some evidence (35)

that small fragments of embryos may also be vernalized. Vernalization of embryos, therefore, is not dependent upon substances received from the endosperm during germination. If substances of a hormone nature are involved in vernalization, they may be manufactured in the embryo itself. PURVIS has shown, however, that whole grains of rye respond more rapidly than do excised embryos and suggests that certain substances received from the endosperm speed up vernalization. CHOLODNY (10) suggests that these substances are auxins or the B vitamins or a certain combination of them.

As far as the author is aware, no one has successfully substituted for the low temperature treatment the application of pure substances or extracts of plant material. The work of MELCHERS (23, 24) with *Hyoscyamus* presents encouraging possibilities in this direction, but more evidence is necessary with other plants before one may be encouraged to postulate that a hormone may be found which, upon application to the plant, may induce vernalization without a low temperature treatment. LANG and MELCHERS (21) suggest that those plants which require vernalization (*i.e.,* a low temperature treatment) do not make the flower-forming hormone prior to vernalization. Subsequent to vernalization they may produce the flower-forming hormone provided environmental conditions are favorable. Presumably such plants will flower without vernalization provided the hormone is supplied from some external source (*i.e.,* from a graft-partner). On such a basis, vernalization simply removes some physiological restriction to the production of the flower-hormone.

Theories Regarding the Mechanism of the Formation of a Flowering Hormone: — Generalizations with respect to the possible action of a flower-forming hormone are difficult because of the variations in response which occur in different species of plants. Various investigators have attempted to correlate the responses of all long-day plants or all short-day plants or all plants of the various classifications on the basis of a given series of reactions of a similar nature. Some postulate the presence of a single flower-forming substance of similar nature in all plants and ascribe the variations in response to given environmental treatments to the influence of these treatments in affecting the rate of synthesis of certain precursors. Critical evaluation of certain theories must await additional research with many different kinds of plants. A review of some of the theories may be of interest from the standpoint of indicating what additional information is necessary before any one theory is to be favored or discarded.

A recent paper by LANG and MELCHERS (21) gives a summary of most of their work with *Hyoscyamus niger.* They have studied two forms of this plant, one of which is an annual and the other a biennial. The biennial form must be exposed to a certain period of low temperature before it may be induced to flower. Subsequent to the low temperature treatment, it apparently reacts in every particular in the same manner as does the annual form. The annual form is a long-day plant. In ten-hour days it remains vegetative, whereas it flowers when the days are over ten hours and forty minutes. Removal of all of the leaves results in the prompt initiation of floral primordia. On the other hand, if one of the

leaves is regrafted to the plant near the growing point, the plant does not flower unless the leaf is exposed to long day. Exposure of an intact plant to a low temperature even under short day results in flowering. Infiltration of the leaves with sugar also results in flowering.

LANG and MELCHERS consider that the annual form and the biennial form subsequent to vernalization fail to flower under short-day conditions because of the removal by the leaves of substances which would ordinarily result in flowering (*i.e.*, a flower-forming hormone). This restrictive influence of the leaves becomes operative only during long, dark periods and apparently is related to exhaustion of carbohydrates in the leaves since the infiltration of the leaves with sugar or the treatment of the leaves with low temperature (a process which might conserve the leaf carbohydrates) removes the restrictive influence. They subscribe to the theory that flowering results from the transmission of a specific stimulus, "florigen," to the growing point. In annual *Hyoscyamus* they believe that this stimulus may be in some way continually supplied—perhaps from the roots or stored in the stem during exposure to light and that during long, dark periods the mature leaves remove this stimulus from the stem, and it does not have an opportunity to accumulate in the growing point and result in floral initiation. They speculate on a mechanism of response for all long-day plants based upon the results obtained with the annual *Hyoscyamus niger*.

The results which have been obtained with *Hyoscyamus niger* have not been obtained, as yet, with other plants. It was noted with several short-day plants (see above) that mature foliage leaves in some way inhibited the transfer of the flowering stimulus when they were exposed to an unfavorable day length. The removal of such leaves often results in the transmission of the stimulus from parts exposed to short day to other branches maintained continually on long day.

CHOLODNY (10) presents the hypothesis that auxin is involved in the flowering processes and the various environmental factors through their action on the synthesis and distribution of auxin determine whether or not a given plant flowers. He reviews the various experiments which indicate the possibility of a "flower-forming hormone." He believes that he could find no evidence to rule out the possibility that auxins were involved in the transition from vegetative to the flowering condition, although he indicates that it may be possible under certain conditions that it is the lack of auxin rather than the presence of auxin which causes this transition. He states, "We must form no hasty conclusion regarding special 'organ-forming substances' . . . . we must first test whether some of the already known phytohormones are endowed with the faculty to induce the physiological effect under observation. . . ." Other investigators have questioned CHOLODNY's hypothesis, and it seems to the author that experimental evidence fails to give it much support.

CHOUARD (11) believes the hormone of flower formation is distinct from auxin. He was able to induce flower formation in the long-day plant, China aster, growing under short days by applying dehydrofolliculin. He postulates that the hormone of flower formation is synthesized in the green leaves only under the action of light but believes that the hormone

is produced in an inactive form and that this inactive form after it reaches a certain concentration limits the production of more of the inactive form. The production of the active form presumably takes place, in short-day plants, only during darkness by a process which is sensitive to temperature and inhibited by light. In long-day plants the light inhibition of the change to active form is presumed to be weak or completely absent.

The evidence that has accumulated for the existence of a flower forming hormone is sufficient to warrant a great deal more work in an attempt to discover just what it is. If there is a single substance, or relatively few substances of similar chemical nature, whose presence in the meristem determines the course of development from the vegetative to the flowering condition in all plants, the importance of discovering the chemical nature of this substance or substances is obvious. The possible practical importance of such a knowledge cannot be overemphasized. In view of the encouraging nature of the results to date, it seems strange that there are not more plant physiologists actively engaged in this field of research at the present time. It is hoped that this present symposium may encourage additional investigators to undertake work in this fascinating field.

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WAVE LENGTH DEPENDENCE AND THE NATURE OF PHOTOPERIODISM

by

H. A. Borthwick,[1] M. W. Parker,[2] *and* S. B. Hendricks[3]

United States Department of Agriculture

Knowledge has been obtained by physical methods about photoreactions that regulate the concentrations of compounds in photoperiodically sensitive plants of both the long-day and short-day types. The action spectrum of a reaction that under certain conditions prevents initiation of flowers by short-day plants has recently been determined with a spectograph specially designed in this laboratory to irradiate entire leaflets at high intensity and with great spectral purity (17, 18). This is the only work of this type from which quantitative results have been obtained. This reaction which opposes floral initiation apparently proceeds in short-day plants any time they receive radiation of suitable quality and quantity, but it actually prevents floral initiation only when irradiation reduces the dark periods below a certain minimal length and when the total energy applied is adequate. For soybean, *Soja max,* var. Biloxi, and cocklebur the minimal length of dark period is between eight and ten hours. In these experiments radiation of known ranges of wave length was applied for short durations near the middle of 14-hour dark periods for soybean and 12-hour dark periods for cocklebur. This procedure divided each of these long dark periods, which were conducive to flowering into two shorter ones neither of which, under the experimental conditions, exceeded the eight to ten hours that were necessary if floral initiation was to occur. By application of various levels of energy to different lots at each region of the spectrum the minimum energy that would prevent floral initiation for each wave band was determined. Action spectrum curves, figure 1, were constructed from data (18).

Two regions of maximum effectiveness for the prevention of floral initiation in these plants were found in the visible spectrum, a narrow one in the violet near 4000 Å. and a rather broad one extending from about 5600 Å. to 7200 Å. in the orange-red region. Minimum effectiveness was found for radiation of about 4800 Å. The long wave length limit of effectiveness was very abrupt at about 7200Å. and infra red was completely ineffective. Radiation at 6400 Å. was about 60 times more effective than that at 4800 Å. for soybean and about 200 times more effective for cocklebur. This difference in ratios for the two plants was mainly the result of lower effectiveness of blue radiation for cocklebur than for soybean.

Experiments of the same type are in progress with long-day plants.

[1] Senior Botanist, [2] Physiologist, Division of Fruit and Vegetable Crops and Diseases, and [3] Principal Chemist, Division of Soils, Fertilizers and Irrigation, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.

Photoperiodic schedules have been found for barley, variety Wintex C. I. no. 6127, in which a brief period of irradiation applied near the middle of each dark period induced spike formation and stem growth. In the absence of such dark period interruption the plants failed to form spikes and remained in the rosette condition. The photoperiodic treatment used in these experiments consisted of 11½-hour photoperiods and 12½-hour dark periods applied in growth chambers (16).

Both the formation and development of spikes and the elongation of stems were induced by interrupting the dark periods with incandescent filament radiation applied for a period as brief as 30 seconds in the middle of each dark period. The energies required to induce spike formation and stem elongation in barley by such treatments were of the same magnitude as those required to prevent floral initiation in Biloxi soybean and cocklebur under closely similar experimental conditions.

Experiments with the spectrograph indicated a spectral region of a high degree of effectiveness in promoting flowering of barley between about 5400Å and 7200Å. The blue end of the spectrum is markedly less effective. Approximately equal flowering response required about 250 fold more energy in the region of 4800Å than in the region of 6400Å. Barley is relatively less responsive than soybean and cocklebur to radiation in the blue violet.

The effects of filtered radiation from various parts of the spectrum on flowering of both long-day and short-day plants have been investigated by a number of workers. RASUMOV (19) and WITHROW and his coworkers (23, 24, 25) found that red radiation very effectively inhibited the flowering of short-day plants and promoted the flowering of long-day ones when used as a supplement to short photoperiods of natural light. They found blue radiation to be ineffective except in the case of china aster, *Callistephus chinensis* var. Heart of France, which WITHROW and BENEDICT (23) found to respond to all wave lengths. KATUNSKIJ (7) and KLESHNIN (8) on the other hand found that all parts of the visible spectrum were effective provided sufficient energy was applied.

FUNKE* (6), working with a large number of plants, found four different types of response to filtered radiation. In one type, red and white radiation were effective but blue was not, a result similar to the findings of RASUMOV and WITHROW. In a second type, white, red, and blue were effective, as was found by KLESHNIN and KATUNSKIJ. In the third type, white was effective but red and blue were not; and in the fourth, blue and white were effective but red was not. FUNKE did not suggest any explanation for the last two types nor can we, in the absence of more complete information as to energies applied, characteristics of filters used, and more detailed knowledge of the behavior of the plants.

Lack of agreement of results of these various workers can be attributed to several causes. Wide differences in energies must be employed to differentiate between effects in different parts of the spectrum. In most instances the failure of a response in the blue part of the spectrum seems to have been the result of inadequate energy. Another reason for lack of agreement seems to have been the fact that the filters used by various workers differed in their light-transmitting characteristics. In general it

* See also his contribution on page 79 of this volume.

was not possible in experiments with filtered radiation to employ narrow and sharply limited bands and at the same time to retain adequate energy. A further source of difference in results probably arose from the type of biological response measured. In most cases the various investigators employed the time required for the production of flowers as a measure of effectiveness of a given treatment. The process of flowering is usually of several weeks' duration, from the time of initiation to the final opening of flowers. It consists of a number of rather distinct phases each of which in different plants may or may not be similarly influenced by a given photoperiodic treatment (5). Different results, therefore, could have been obtained from different plants. In the work of this laboratory the biological response measured has been limited to floral initiation and all of the results have been obtained from dissections of the experimental plants within a week after conclusion of the treatments. By means of the spectrograph narrow wave length bands of very pure radiation have been obtained and with a carbon arc adequate energy has been available throughout the visible.

Experimental evidence for the basic theory that flowering is controlled by a hormone-like material produced in the leaf is given in papers cited by MURNEEK (13). Although LANG and MELCHERS' observation (9) that flowering in *Hyoscyamus niger* can be induced by defoliation may suggest that the leaf is not the locus of the photoperiodic reaction, a quite different interpretation is advanced below which reconciles their results with other data. Evidence that flowering is regulated by means of a hormone-like material, however, is hypothetical and will probably remain so until some type of assay is devised.

The reactions that cause floral initiation in short-day plants might at first appear unrelated to those that cause initiation in long-day ones. Several workers, however, have been led by their experiments to advance the idea that both types of plants are similar in underlying processes of initiation. Thus WITHROW and WITHROW (25) state: "The photo-activated molecule involved in photoperiodism is probably the same for both long-day and short-day plants since the same general regions of radiation are effective in producing their respective responses." FUNKE (6) also recognized a basic similarity of the two types of plants in their response to different colors of light. This essentially is the concept back of ČAJLACHJAN's (3) introduction of the term "florigen" for the "flower forming hormone" although an interrelationship of long-day and short-day plants is not shown by his work. MELCHERS (10) induced a short-day plant, Maryland Mammoth tobacco, to flower on long-day by grafting a leaf of a long-day plant, annual *Hyoscyamus niger,* to it and thus showed that material derived from the latter could bring about flowering of the former. CHOLODNY (4) was careful to emphasize that this type of result indicated that a material controlling flowering in one plant is effective in another even of different genus but did not require the flower inducing materials to be identical.

The concept that long-day and short-day plants are basically similar in photoperiodic response is strongly supported by other experiments that have been described and by current work in this laboratory. The action spectra obtained in the latter work give a quantitative expression to results that were qualitatively anticipated by KATUNSKIJ (7) and by KLESHNIN

(8). Thus the wave length region of light that is most effective in preventing floral initiation of short-day plants when applied near the middle of the dark period is most effective in causing floral initiation of long-day plants. Radiant energies at a particular wave length for effecting control of soybean (short-day) and barley (long-day) are moreover of the same order of magnitude.

Plants that are closely related often exhibit different photoperiodic responses. Genera of plants, such as *Nicotiana,* contain both short-day and indeterminate species. Certain species, such as soybean (*Soja max*), contain varieties that flower only with short photoperiods and others that flower over a wide range of photoperiods, and some even with continuous light. These last varieties are sometimes erroneously spoken of as indeterminate but they are more accurately to be described as short-day types because they flower much sooner with short photoperiods than with long. Although data are not available it seems probable that within long-day plants there may also be considerable variability in the range of photoperiods on which the various types will flower.

In the case of a grass, *Bouteloua curtipendula,* OLMSTED (14, 15) was able to isolate clones from different latitudes that varied from short-day to long-day type of response. Such observations suggest a close relationship between the reactions of long-day and short-day plants.

Experiments indicate that effects taking place in the dark period are primarily responsible for control of flowering in both long-day and short-day plants. The significance of the dark period in regulation of flowering is demonstrated by the effectiveness with which irradiation for short times near the middle of dark periods prevents flowering of short-day plants or causes flowering of long-day plants. It is also illustrated by the fact that flowering cannot be induced in long-day plants that received photoperiodic cycles of 24 hours or less if the dark periods of those cycles exceed a certain critical length, nor in short-day plants on cycles of any length unless a critical length of dark period is exceeded. In both cases the length of the uninterrupted period of darkness is critical.

An hypothesis that is useful to guide design of experiment, that recognizes established facts, and that is in harmony with fundamental similarity in the behaviour of long-day and short-day plants is the following:

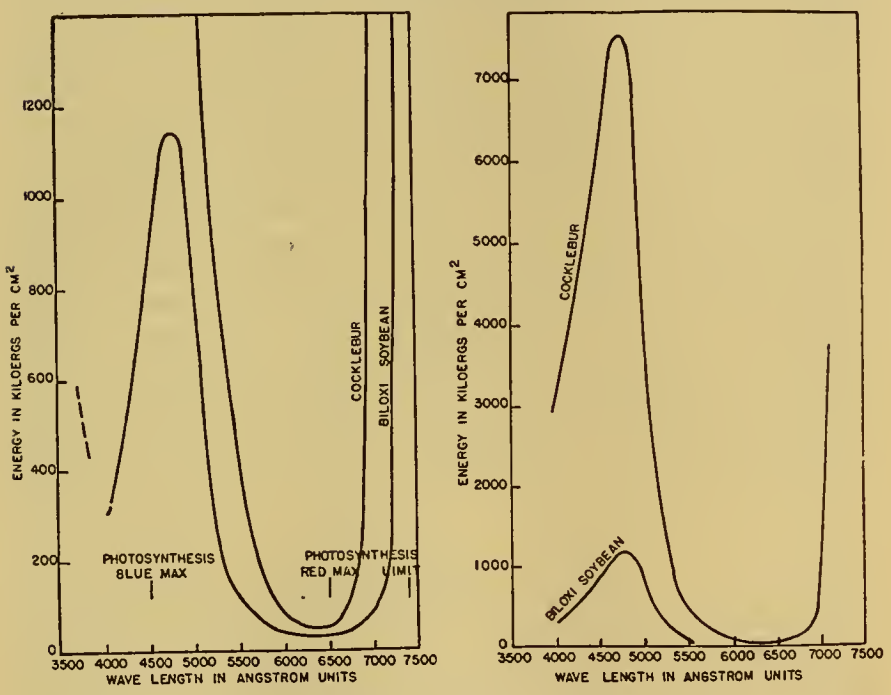
> *Floral initiation is controlled by an active substance produced in the leaves of the plant. This substance or an intermediate in the course of its production is subject to photosensitized destruction in the leaf. The active substance must reach an adequate concentration to cause floral initiation but is inhibitory at relatively higher concentrations.*

The hypothesis is independent of the specific type of pigment responsible for the action spectrum and is not concerned with the nature of the active substance or the reactions involved in determining the type of structures differentiated from the meristematic tissues.

Observed types of photoperiodic response in plants are corollary to this hypothesis. Thus it would follow that short-day plants are those in which the concentration of the active substance derived from illuminated leaves is insufficient to cause floral initiation but exceeds the critical value after a dark period of sufficient duration. In long-day plants enough active sub-

stance escapes photosensitized destruction, even in continuously illuminated leaves, to cause floral initiation; and an inhibiting concentration is reached after an adequate dark period. Light, accordingly, acts through the same mechanism in both cases, that is, possibly to destroy the same compound by a photosensitized reaction. It is of interest in this connection that MELCHERS and LANG (12) postulated a reaction in the leaves of *Hyoscyamus* that inhibits floral initiation.

Intermediate type plants that flower only when the day is adequately long but not too long, have chiefly been described by ALLARD (1). Some



Composite action spectrum curves showing the energy required at various wave lengths for the suppression of floral initiation in soybean and cocklebur (18).

examples are *Mikania scandens, Phaseolus polystachios, Eupatorium torreyanum,* and a New Guinea form of *Saccharum spontaneum.* The last of these is most striking in flowering only for day lengths within the range of 12 to 14 hours. These plants, described in terms of the above hypothesis, are ones in which concentrations of the active substance produced under continuous light are insufficient to cause floral initiation and in which inhibiting concentrations are reached after an adequate dark period.

Indeterminate plants can be considered as those in which adequate concentrations of the active substance are produced in continuous light and limiting values are not exceeded during dark. Floral initiation by plants of this class might be most effective for continuous light, intermediate periods, or for short days in which case similarity to one of the above three classes would be indicated.

Only one other type of photoperiodic response in plants is suggested by the hypothesis, namely, failure of floral initiation under any condition.

This could be due to an excess of the active substance even in continuous light or failure to reach the threshold concentration after the maximum permissible dark period. At the present time examples of such cases cannot be sought with any confidence because photoperiodic conditions are by no means the only ones to be satisfied in floral initiation. Experiments with sugar beets (22) and biennial *Hyoscyamus* (11), however, suggest either that adequate concentrations are not attained in such plants in the first year or that some other controlling factor has not then been removed.

Information about the leaf pigment responsible for photoperiodic control of flowering is given by the action curve, irrespective of any hypothesis about active substances and mechanisms of control. For a number of reasons, however, the action spectrum cannot simply reflect the absorption curve of a leaf pigment. Chlorophyll and carotenoids, the principal leaf pigments are present in sufficient amounts greatly to reduce the intensity of most wave lengths of visible radiation deep in the leaf (21). An action curve thus will reflect the screening action of such pigments even though they do not take part in the effective photochemical reactions.

At first sight it would appear that photosynthesis, despite constant quantum efficiency across the spectrum, would be greatly reduced in a leaf in regions where chlorophyll has a low absorption coefficient. Actually most leaves contain sufficient chloroplasts to make about equal photosynthetic use of all visible radiation. Consequently photosynthetic use of strongly absorbed radiation, as in the blue, chiefly takes place near the surface of chloroplast-containing tissue. Weakly absorbed radiation, as in the green, also is most effective at the surface but increases in importance, relative to more strongly absorbed radiation, and at sufficient depth it may become the most effective. This condition is illustrated by Seybold (20). As a natural phenomenon the absorption process and leaf structure give efficient use of the incident light, since in photosynthesis it is probably unimportant, over small distance, exactly where the reaction takes place.

If chlorophyll is involved either directly or as a screening pigment in some other photochemical process in a leaf, in which control of a process has to be effected throughout the absorbing tissue then the self screening becomes most important. In fact the paradoxical situation can be met where the most strongly absorbed radiation is least effective.

Four features of the photoperiodic action curve indicate that chlorophyll may be playing an important part in the process. These are:

a) All regions of the visible spectrum are effective.

b) The limit of effectiveness in the red is the same within limits of experimental measurement as the absorption limit of chlorophyll in leaves.

c) The region of maximum response is near the position of red absorption maximum for chlorophyll.

d) The region of greatest change in response, 4900 to 5400 Å., is the region in which the absorption coefficients of chlorophyll change most rapidly.

Low photoperiodic effectiveness for radiation in the blue is not in apparent agreement with chlorophyll being the effective pigment, even when screening by high absorption in the chloroplasts is considered. According to present concepts the red fluorescence of chlorophyll irradiated in the blue

is due to the high probability of transition from the blue to the red excited levels. Energy derived from the long lived red states alone is thought to be effective in photosynthesis.

Another interpretation of the action spectra is that the effective pigment absorbs strongly only in the yellow-red. This would require a blue pigment unless intense photoperiodically-ineffective absorptions are present elsewhere in the visible portion of the spectrum. The pigment, chlorophyll or unknown, could act by transfer of absorbed energy to a reaction underlying formation of the effective compound in the leaf. Such reactions are well known and are said to be photosensitized. Products leading to the active substance or the substance itself must remain for several hours within the leaf cells in which they were formed, possibly closely associated with chloroplasts, because brief periods of irradiation after several hours of darkness have elapsed would not otherwise be effective.

Action spectrum curves for the photoperiodic response of several more plants are needed to increase our assurance that the facts reported in this paper concerning such data are common to all such plants. These additional data however, will probably not lead us to an identification of the compound that is active in the photoperiodic process. This step must apparently await the development of a biological assay, an achievement that at the moment seems beset with great difficulties.

The hypothesis proposed in this paper to explain the photoperiodic reaction has been useful in designing the action spectrum experiments and interpreting the results of various photoperiodic investigations reported in the literature. If it should stimulate work that may either lend it further support or disprove it, the hypothesis will have served an additional useful purpose.

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Note Added in Page Proof.— Important experimental advances have been made recently, after the preceding article was written. The action spectrum for spike formation in Winter barley has been completely worked out by H. A. Borthwick, S. B. Hendricks, and M. W. Parker, who will report shortly about this in the Botanical Gazette, comparing it with curves for cocklebur and soybean. Essential similarity of the various curves is clearcut requiring the same pigment or closely related pigments as the initial absorber of the radiant energy in these long- and short-day plants. In barley, moreover, the action curve for stem elongation is identical with that for floral initiation. This indicates that the two processes are integrally associated.

Still greater interest attaches to the action spectrum for leaf elongation and internode shortening in etiolated pea seedlings. Results of WENT (Am. Jour. Bot. 28:83-95, 1941) on effects of light on stem and leaf growth of etiolated pea seedlings indicated that the action spectrum might resemble that of photoperiodism. This is borne out by a detailed determination made in association with Dr. WENT of the action curve for leaf elongation in etiolated pea seedlings, use being made of the spectrograph designed for the work in floral initiation. In this work peas (variety Little Marvel) were grown in sand culture in complete darkness for three days and then illuminated with radiation of the various wave lengths at definite energies for four minutes on each of the succeeding four days. The peas were harvested on the ninth day and the lengths of the first and second leaves and the various internodes were measured. From these data energies required to give a definite leaf length at the different wave lengths were determined. The response is similar in detail to that of floral initiation.

Pea seedlings grown in complete darkness produce no chlorophyll. The leaves are yellowish in color and the internode at the time it begins to elongate also has a slight yellow coloration. The effective pigment, however, must absorb in the red and thus is not the apparent one, but rather must be minor in its contribution to the color of the slightly pigmented seedlings. Nevertheless this plant material offers the greatest hope for identification of the effective pigment since the dominating chlorophylls and carotenoids of normal leaves are absent.

A fundamental similarity in controlling mechanism is thus established between floral initiation of long- and short-day plants, of stem elongation in long-day plants, of leaf elongation, and of internode shortening in etiolated pea seedlings. Naturally one wonders what other phenomena of growth are controlled through this same mechanism and one looks more deeply for the nature of the mechanism itself than merely effect upon a meristem.

We might hazard the speculation that a property of the protoplasm in the leaf, subject to change by a photochemical process, operates as the controlling mechanism.

THE PHOTOPERIODICITY OF FLOWERING UNDER SHORT DAY WITH SUPPLEMENTAL LIGHT OF DIFFERENT WAVE LENGTHS

by

G. L. FUNKE †

Late Director, Botanical Institute, University of Ghent

From 1936 till 1940 in Ghent, Belgium, from 1941 till 1945 in Leyden, Holland, and again since 1946 in Ghent, I investigated the effect of photoperiodicity on flowering of a large number of plant species in different ranges of wave length (3-13). The plants receive full daylight from 7 a.m. till 3 p.m.; for the rest of the day they are covered, partly by dark cases, partly by white (limed), red and blue glass; check plants remain in the open air. The different sorts of glass transmit approximately an equal quantity of solar energy. The place of experiment is such that during the hours when the plants are covered, the sun does not shine directly upon the glass. Temperature and humidity of the air under the glass cases, therefore, are only slightly different from those outside; yet flowering under the white glass is exceptionally a few days earlier than with the check plants, owing to a little more favorable conditions during the night. The difference in time of flowering due to the different wave lengths varies between 7 days and more than 3 months.

"Dark" or D means plants which get full day light from 7 a.m. till 3 p.m.; "red" or R, "blue" or B and "White" or W means plants which are exposed to full daylight from 7 a.m. till 3 p.m. and to red, blue and white light respectively from sunrise till 7 a.m. and from 3 p.m. till sunset.

Up till now I have examined more than 100 species and varieties. Some species proved to be photoperiodically indifferent (group 0 in the list); the others can be divided into four groups according to their reactions, while a few species behave in a way which so far I have not been able to explain. My results deviate on the whole from those of other authors (1, 16, 17, 19, 21, 23, 24, 25, 26); as my way of experimenting is very different from theirs, a comparison is hardly possible for the moment.

Group I: [W-R] [B-D]: "red" flowers at the same time as "white," "blue" at the same time as "dark"; the flowering of long day plants is favored by a long white as well as by a long red day; "blue" and "dark" hasten the flowering of short day plants.

It may happen that a long day plant develops a few flower buds in B, which, however, decay or which, exceptionally, open after an abnormally long time and develop crippled flowers (6, 8, 12); these flowers yield only a few viable seeds if at all. A striking example of this phenomenon is presented by *Anthemis tinctoria*. This species is a LL-plant (2, 14, 18) which needs a long red day for normal flowering, whilst a long blue day is hardly sufficient for the formation of a few flower buds. I think this is the first case

we have seen in which the different ranges of wave length have a different influence on the stages of reproduction.

TABLE 1: *List of Species* (species belonging to the Cruciferae have been given in italics; S = short day plant; L = long day plant): —

GROUP O, PHOTOPERIODICALLY INDIFFERENT:

Aethionema saxatile
Alonsoa warswiczii
Biscutella auriculata
Calceolaria pinnata
Cardamine pratensis
Doronicum pardalianches
Erucastrum obtusangulum
Erysimum cheiranthoides
Loasa vulcanica
Taraxacum officinale
Teucrium scordium
Thlaspi arvense

INTERMEDIARY BETWEEN O AND IV:

Biscutella laevigata
Sisymbrium irio

GROUP I [W-R] [B-D]:

Anthemis tinctoria L
Aster ericoides S
Aster linosyris S
Aster multiflorus S
Callistephus sinensis S
Campanula persicifolia L
Campanula phyctidocalyx L
Campanula rotundifolia L
Centaurea montana L
Cosmos bipinnatus S
Dianthus barbatus L
Fuchsia hybrida L
Glycine hispida S
Glycine soja S
Hedera amorensis S
Hedera colchica S
Helichrysum bracteatum L
Heliotropium peruvianum
Lactuca sativa L
Lycopus europaeus L
Lysimachia ciliata L
Matricaria eximia nana L
Mentha silvestris L
Plectranthus purpureus S
Sedum kamtschaticum L
Solidago virgaurea S

INTERMEDIARY BETWEEN I AND II:

Chrysanthemum indicum (8 var.) S
Hypochoeris radicata L
Salvia glutinosa S

GROUP II [W-R-B] [D]:

Achillea millefolium L
Alyssum maritimum L
Argyratum mexicanum L
Azalea indica L
Brunella vulgaris L
Camelia japonica S
Centaurea cyanus L
Eschscholtzia californica L
Iberis umbellata L
Lobelia erinus L
Malcolmia maritima L
Matricaria chamomilla L
Matricaria inodora L
Matthiola incana L
Mentha rotundifolia L
Mimulus luteus L
Ocimum basillicum L
Oxalis martiana L
Perilla nankinensis S
Plectranthus fruticosus L
Rudbeckia speciosa L
Salvia runcinata L
Scrophularia nodosa L
Sedum aizoon L
Sedum selskianum L
Sedum spectabile L
Sedum telephium
Silene inflata L
Statice puberula L
Teucrium chamaedrys L
Trifolium pratense L
Turritis glabra L
Veronica chamaedrys L

GROUP III [W] [R-B-D]:

Gnaphalium lanceolatum L
Lepidium draba L

GROUP IV [W-B] [R-D]

Aethionema cappadocicum L
Aethionema diatrophis L
Aethionema grandiflorum L
Alyssum calycinum L
Anastatica hierochuntica L
Berteroa incana L
Brassica nigra L
Camelina sativa L
Cheiranthus allionii S
Crambe hispanica L
Iberis amara L
Iberis intermedia L
Nasturtium silvestre L
Neslea paniculata L
Raphanus caudatus L
Raphanus sativus L
Sinapis alba L
Sisymbrium sophia L

Group II: [W-R-B] [D]: "red" and "blue" flower at the same time as "white"; the colour of the light is of no importance. Between groups I, II and III all sorts of transitional cases occur.

Group III: [W] [R-B-D]: flowering of long day plants only in "white"; neither red nor blue rays have any furthering effect; *vice versa* for short day plants. As R and B can act separately as darkness (groups I and IV), it is theoretically possible that they can do so both at the same time; nevertheless only 2 species belonging to this group have been found up till now.

Group IV: [W-B] [R-D]: the opposite of group I; "blue" flowers at the same time as "white," "red" at the same time as "dark." This group seems to stand by itself; all species which in my experiments were found to belong to it are *Cruciferae;* however, other members of this family belong to groups 0, II or III. I think it remarkable that none of the *Cruciferae* investigated so far belongs to group I, and the more so because otherwise there is no indication of a relation between systematic position and photoperiodical reaction. Indeed, it will be seen in the list that there are many examples of genera whose species belong to different groups.

Practically without exception it is to be stated that the photoperiod acts differently on the reproduction and on the longitudinal growth. When *e.g.* a long day species of group I is considered, the specimens in D and B remain vegetative, but those in D are always very short whilst in B the normal length is reached. One of the few exceptions is presented by *Campanula rotundifolia.* Therefore I think that an investigation into the influence of photoperiod on auxin formation is urgently needed (20, 22) and could elucidate many obscurities in this field.

This is especially the case for the phenomenon of reversibility induced by photoperiod (9, 10, 12). *Perilla acymoides* and *P. acymoides* var. *nankinensis,* especially *nankinensis,* are extreme types of short day plants belonging to group II. In natural day length they remain vegetative till the end of September. When the natural illumination is interrupted in May by a small number of short photoperiods they blossom in the middle of the summer and afterwards they show the reaction of reversibility, that is, the axes of the inflorescences resume their vegetative growth; towards the end of the season a second flowering stage follows. There seems to exist an equilibrium between the formation of florigen during short days and of auxins during long days. A large quantity of florigen, due to a great number of short photoperiods, checks the formation of auxins with the consequence that after the first flowering stage growth is not resumed and the life-cycle comes to an end. *Ocymoides* is more sensitive in this respect than *nankinensis;* in the former 7 short days determine the premature flowering, reversal and second flower-

ing; 14 short periods induce premature flowering, but prevent the reversal, the plants die; in the latter variety 7 short days have no influence, but 14 determine the onset of flowering, reversal and second reproductive stage.

For particulars about the treated species and for the discussion of literature I must refer to my former papers.

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NUTRITION AND METABOLISM AS RELATED TO PHOTOPERIODISM

by

A. E. MURNEEK

University of Missouri, Columbia, Missouri

In consideration of the relationships between nutrition and metabolism and sexual reproduction as effected by the photoperiod, one should distinguish clearly the various stages of reproduction, from inception of floral primordia to flowering and fruit production. Unfortunately this has not been done in the vast majority of instances in nutritional studies and interpretation of chemical analyses of plants. Moreover, in sampling material for chemical assays one should keep in mind the fact, so aptly stated by LOEHWING (13) that at any given time similar organs of a plant may be in various stages of development. Parts of the tissues on the same plant or portions thereof may range from juvenile to senescent states and through all stages of reproductive development. This is particularly true of plants with an indeterminate type of growth. Disregarding of these facts, as in chemical analysis of whole plants or large portions of them, has resulted in accumulation of recorded data that are difficult or impossible to interpret and therefore of little value.

Most of the earlier nutritional and chemical studies on photoperiodism were influenced by or interpreted by means of the carbohydrate-nitrogen relationship concept, which was advanced by KLEBS and re-emphasized by KRAUS and KRAYBILL shortly before the announcement of the discovery of photoperiodism. Plants exposed to certain lengths of day have been grown under various regimes of soil nutrient supply with particular emphasis on nitrogen and the observed results, as regards time and amount of flower development roughly recorded. In many instances concomitant chemical analyses for carbohydrates and nitrogen compounds have been made. The results of the earlier work have been reviewed critically by the writer and others and therefore need not be recapitulated here (MURNEEK, 21, 22; LOEHWING, 12, 13). In general the information thus secured is very conflicting and concerns largely observations of plants in comparatively late stages of vegetative and reproductive development. Therefore, it is very little, if at all, applicable to the problem of relation of nutrition and metabolism to induction of the sexual state by the photoperiod. The evidence, however, is indicative to some extent of the nutritive states of plants in various stages of flowering and fruiting (if definitely specified), at which condition in most instances the plants were sampled.

Some relatively recent studies on nitrogen nutrition in relation to photoperiodism should be referred to here. In her investigation with several long- and short-day plants, including *Soja* and *Xanthium,* WITHROW (31) comes to the conclusion that the external nitrogen supply is not as determining a

factor in floral initiation as the photoperiod or temperature but that the time of appearance of visible floral buds was altered by it in some species. PARKER and BORTHWICK (28) found that in Biloxi soybeans at the end of the induction period (1 week), the total and soluble non-protein nitrogen concentration was higher in the reproductive than the vegetative control plants. This is a confirmation of the results obtained with the same plant by the writer (21). They state that the differences in chemical composition of plants did not seem to have any causal relationship to flower initiation. From their observations of *Xanthium pennsylvanicum* plants, grown in nutrient solutions of high or low NPK content or with or without an external supply of N, NEIDLE (26) and NAYLOR (25) conclude that the amount of nitrogen in the nutrient medium had no definite effect on response to the photoperiod and that plants low in NPK had the same critical day-length requirements as those supplied amply with these soil nutrients. When given abundant N more burrs were produced on *Xanthium* plants, however. Similarly a larger crop of seeds was set by guayule plants that received the highest concentration of nitrogen (MITCHELL, 16).

From his sand-nutrient-solution cultures of several kinds of plants ČAJLACHJAN (3, 4) concludes, likewise, that no variation in mineral nutrition used could change plants from a vegetative to the reproductive state and that contrary to the adopted idea that a large increase in nitrogen supply prevents plants from entering the flowering and fruiting phase, frequently nitrogen stimulates this process. Both long- and short-day plants reacted similarly to nitrogen nutrition. In another experiment, while exposing *Perilla nankiensis* and *Chrysanthemum indicum* plants to various photoperiods, he immersed the leaves into .5 and 1.0% solutions of $NaNO_3$, KNO_3, NH_4NO_3, asparagin and glucose, respectively, for one hour every few days and, in addition, applied to the soil nitrates. The results seemed to indicate that, if anything, extra supply of nitrogen was favorable to flowering and that any possible carbohydrate-nitrogen relationship has no bearing on induction of reproduction (ČAJLACHJAN, 5). Considering the above cited and much other evidence, it appears that nitrogen is one of the most crucial nutrient elements in initiation of sexual reproduction and that it often is a limiting factor in the production of fruits and seeds (MURNEEK, 17, 19).

One is reminded here of KLEBS' experience with *Sempervivum funkii* plants, which would not flower in winter and lead him to remark that "aber niemals gelang es Blüten im Winter zu erzeugen, *obwohl die blühreifen Rosetten bereits im Herbst alle nötigen organischen Stoffe aufgespeichert enthalten.*" By exposing the plants for a few days to continuous electric light (increase in length of day) they produced flowers, while quite similar non-exposed plants, kept in the same greenhouse, did not bloom (KLEBS, 10, p. 27).

Photoperiodism, as regards the induction of reproduction, does not seem to stand in any direct quantitative relationship to carbon assimilation for: *a*) It may occur in very weak light, which does not permit much photosynthesis and during which respiration probably is in excess of carbohydrate synthesis. *b*) Drastic reduction in the length of day, which would

seem to curtail greatly the diurnal production of carbohydrates, usually leads to initiation of flowers in the case of many short-day plants.

Nevertheless carbon assimilation may possibly be connected, in one way or another, with the photoperiodically induced stimulus in the leaves. PARKER and BORTHWICK (29) have shown that induction does not occur when plants are deprived of carbon dioxide, without which it may not take place in a leaf even though satisfactory conditions for photosynthesis prevailed elsewhere in the plant (HARDER and WITSCH, 8). When the long-day plant *Hyoscyamus niger* is submitted to short-day exposure flower induction is inhibited. As this (inhibition) seemed to have occurred in darkness, it suggested to MELCHERS and CLAES (15) that a dissimilation process may be involved which destroys a possible carbohydrate precursor of the flower hormone ("florigen"). This idea was tested further by keeping the plants during ½-⅔ of the dark period in an atmosphere of N_2 or CO_2. Because of this treatment flower initiation was inhibited, which evidently was in support of their hypothesis. When sugar was supplied by means of leaf infiltration, flowering also occurred under short-day exposure.

Experimental work with *Bidens tripartitus* has indicated to POTAPENKO (30) that photoperiodic induction has no direct relationship to photosynthesis but that elimination of light during the dark phase seems to "restitute the working capacity of the chloroplasts" so that their assimilation may be enhanced during the following light phase.

Assimilation and respiration were determined manometrically in leaves of *Kalanchoe blossfeldiana* under short- and long-day exposures by BODE (2). The reproductive short-day plants had at the time of flower bud development, higher photosynthesis and respiration rates. Chloroplast pigments also increased during the short-day exposure. This is in agreement with some observations made by the writer on short-day soybean (Biloxi) plants (MURNEEK, 21). It should be of interest to note here that as Biloxi plants become reproductive, as a result of exposure to appropriate photoperiods, there is an augmentation in carotene and xanthophyll contents of the leaves. This may possibly have some connection with sexual reproduction in this plant (MURNEEK, 20, 23).

The idea proposed by GRAINGER (6) that flower induction is influenced by the rate of nocturnal translocation of carbohydrates from the leaves to the growing points, not only lacks confirmation but is contradicted to a considerable extent by his further studies with *Anemone, Epilobium, Lupinus, Lysimachia* and *Vaccinium* wherein he shows that production of flower initials requires very little carbohydrates but only "pledge" a considerable amount for future requirements (GRAINGER, 7).

The writer has conducted extensive investigations on the relation of chemical composition to photoperiodism using several kinds of plants, but chiefly the now popular Biloxi soybean, for this purpose (21). Instead of analysing plants during comparatively late stages of flower formation, as had been done heretofore, he followed their chemical composition, as regards nitrogen and carbohydrate content, in various parts throughout the course of vegetative and reproductive development. The plants were grown in rich soil and, beginning on the third day of emergence above ground,

TABLE 1: *Changes in total nitrogen content of soybean plants, var. Biloxi:* —

AGE—DAYS	Percentage on Dry Weight Basis			
	Stems		Leaves	
2	7.51		.....	
	Long	Short	Long	Short
6	8.15	8.96	8.17	8.93
12	6.44	7.52	6.40	7.79
20	3.73	4.87	5.82	6.80
27a*	3.33	4.02	5.24	5.74
33b	3.04	3.61	4.54	4.80
40c	2.75	3.13 (Pods 5.16)	3.82	4.20
80d	1.55	3.77 (Pods 4.90)	2.39	4.88

* *a* — Flower buds on short-day plants.
b — Flowers on short-day plants.
c — Flowers and small pods on short-day plants.
d — Pods of various sizes on short-day plants.

exposed respectively to long (14 hour) and short (7 hour) photoperiods. Results of analyses of stems and leaves are presented in table 1.

It will be observed that the short-day or reproductive plants, while growing in the same soil medium, had a considerably higher nitrogen concentration from the time of inception of floral primordia (sixth to twelfth days) till flowering and even during early fruiting. This was true of both the leaves and stems, but particularly so of the latter. This is in agreement with the results reported by KNODEL (11), by ASAMI and ITO (1) and subsequently by others (PARKER and BORTHWICK, 28).

The augmented nitrogen content of the short-day plants, in comparison to the long-day ones, was due to an early and continued inhibition of their

TABLE 2: *Rate of stem elongation of soybean plants, var. Biloxi. Height in centimeters:* —

AGE, IN DAYS	*Long-day Plants*	*Short-day Plants*
	(cm.)	(cm.)
2	4	4
6	10	10
12	18	17
20	25	20
27	33	21
33	42	21
40	48	21

growth in height (photoperiodic inhibition), as is evident from table 2. On the 12th day the plants were already measurably shorter in stature. As vegetative growth is curtailed, and no impediment in absorption of soil nutrients and in organic synthesis, nitrogenous and other compounds accumulated in the plants. That there was an accretion of carbohydrates, especially starch, similarly to nitrogen, is shown in table 3. The plants were exposed to the respective photoperiods, as was stated before, on the 3rd

FIG. 3.—A vegetative Biloxi soybean plant, 42 days old, grown under a long (14 hour) photoperiod. Continuous vegetative extension of stem.—Photographs by the author.

FIG. 4.—A reproductive Biloxi soybean plant, 42 days old, grown under a short (7 hour) photoperiod. Terminal extension had ceased 15 days before photo was taken. Numerous short axillary shoots.

FIG. 5.—Close-up of upper part of stem of reproductive plant shown in Fig. 4. Numerous pods, flowers and buds on short axillary shoots. No terminal extension of stem (photoperiodic inhibition).

FIG. 6.—Section through the apical meristem of a vegetative soybean plant (14-hour photoperiod), × 120. Note rounded tip.

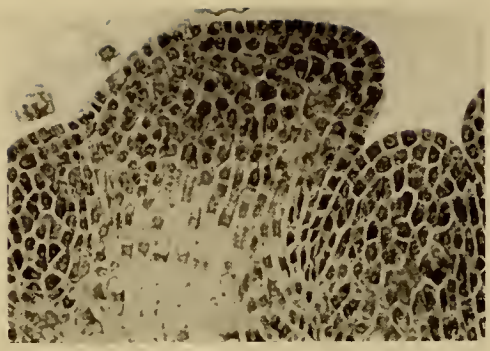

FIG. 7. Section through the apical meristem of a reproductive soybean plant (7-hour photoperiod), × 120. Note flattened tip, the first microscopically visible sign of induction of reproduction, and prominent axillary meristem. Photographs by the author.—Cf. p. 57.

FIG. 8. *Rudbeckia bicolor* plants, 86 days old. On right, vegetative plant rosette with extremely inhibited stem photoperiodic inhibition (short days). On left, reproductive plant, with full development of stem (long days).—Cf. p. 49.

FIG. 9. High temperature induced flowering in *Rudbeckia bicolor* plants grown in a relatively hot greenhouse. On right, reproductive plant (long days and high temperature). On left, reproductive plant (short days and high temperature). Note inhibited stem elongation photoperiodic inhibition, but induction of reproduction, by relatively high temperature.

day, therefore those 6 days old had received 4 photoperiods, those 12 days old 10, etc. All carbohydrates are expressed as glucose. Under "total carbohydrates" is understood the sum of total sugars, starch and so-called hemicelluloses.

TABLE 3: *Effects of photoperiod on carbohydrate metabolism of soybean plants, var. Biloxi—in percentages of dry weight: —*

DESCRIPTION OF PLANT MATERIAL	TOTAL SUGARS		STARCH		TOTAL CARBOHYDRATES	
Plants 2 days old						
Stems	3.16		3.57		25.95	
Cotyledons	7.28		.32		24.10	
	Long day	Short day	Long day	Short day	Long day	Short day
Plants 6 days old (2 + 4 days)						
Stems	2.52	2.35	2.13	1.08	21.25	12.52
Leaves	2.03	1.70	.84	.84	10.93	9.72
Cotyledons	1.70	2.52	.58	.00	13.32	11.09
Plants 12 days old (2 + 10 days)						
Stems	1.87	1.35	1.18	1.56	13.85	10.19
Leaves	1.88	1.22	1.69	1.65	12.05	18.29
Cotyledons	2.17	2.22	.92	1.00	18.82	17.54
Plants 20 days old (2 + 18 days)						
Stems	1.71	1.65	1.16	1.26	12.43	17.13
Leaves	1.87	1.09	2.13	1.00	17.23	12.17
Plants 27 days old (2 + 25 days)						
Stems	1.16	1.32	.35	1.24	14.98	18.80
Leaves	1.96	2.52	1.16	.85	15.76	14.65
Plants 33 days old (2 + 31 days)						
Stems	3.49	1.74	3.25	9.80	23.45	26.06
Leaves	6.45	4.47	4.55	3.82	25.62	19.09
Plants 40 days old (2 + 38 days)						
Stems	3.49	4.24	6.04	19.58	29.75	42.55
Leaves	5.77	4.33	10.56	12.54	32.06	32.60

As one would anticipate, the curtailed growth in height of the plants seems to have affected also changes in enzyme activity (HIBBARD, 9), which probably preceded the accumulation of organic materials.

While the initiation of the sexual state is most likely the function of a special catalytic substance (hormone), the rapid increase in food substances may be considered a kind of assurance of nutrition for the developing flowers, but especially the fruit and seeds. The proper development of the reproductive organs and associated tissues and the successful setting of seeds and their growth depends very much upon the food reserves of the plant, chiefly on the various nitrogen and carbohydrate compounds. Lacking an ample food supply, flowers will not develop and set fruit normally, certainly not in large numbers.

From the evidence at hand it is not clear whether in the soybean (Biloxi) the reduced photoperiod (7-hour day) effects independently induction of reproduction and inhibition of vegetative growth. There is the possibility that a special catalytic substance may be produced by the young floral organs, which inhibits stem elongation. Reduction in growth probably started considerably before the 12th day, which was somewhere near

the end of the induction period, considering most of the flower initials. Assuming this to be the case, and considering observations on other plants, growth in height then may be inhibited during at least the following stages of sexual reproduction: *a*) While floral primordia are initiated (*Soja,* etc.), *b*) while the plant is in full bloom (*Zea, Triticum, Cucumis,* etc.) and *c*) during the period of fruit and seed development (*Lycopersicon, Cucumis,* etc.).

In all instances it is the reproductive organs, in one stage of development or another, that seem to control metabolism and growth of the plant, once a state of intense reproduction is initiated and environmental conditions are favorable for its maintenance. Since plants that have become highly reproductive require large amounts of food for seed and fruit development, and as these substances are used also for the formation of vegetative tissues, though not necessarily in the same proportion, one can see the value of a mechanism in the plant that would lead to curtailment of vegetative growth and consequent diversion, storage and supply of certain materials for the growth of embryos and accessory structures (MURNEEK, 22; LOEHWING, 13; WOLFE *et al.*, 34; NOVIKOV, 27).

TABLE 4: *Carbohydrate-nitrogen relationships (ratios) in stems of soybean plants, var. Biloxi, when grown under certain photoperiods:* —

DESCRIPTION OF PLANT MATERIAL	SUGAR N	STARCH N	SUGAR AND STARCH N	TOTAL C-H* N
Plants 2 days old				
Before exposure to photoperiod. Whole stem	.42	.48	.90	3.25
Plants 6 days old (2 + 4 days)				
Long-day, height 10 cm. Whole stem	.31	.26	.57	2.61
Short-day, height 10 cm. Whole stem	.26	.12	.38	1.40
(Beginning of induction of reproduction.)				
Plant 12 days old (2 + 10 days)				
Long-day, height 17 cm. Whole stem	.29	.18	.47	2.15
Short-day, height 17 cm. Whole stem	.18	.21	.39	1.36
(Induction probably completed.)				
Plants 20 days old (2 + 18 days)				
Long-day, height 24 cm. Whole stem	.46	.31	.77	3.33
Short-day, height 20 cm. Whole stem	.14	.26	.40	3.34
(Primordia formed, but no visible flower buds. Growth inhibited.)				
Plants 27 days old (2 + 25 days)				
Long-day, height 32 cm. Whole stem	.35	.10	.45	4.50
Short-day, height 21 cm. Whole stem	.34	.30	.64	4.68
(Flower buds distinct.)				
Plants 33 days old (2 + 31 days)				
Long-day, height 41 cm. Whole stem	1.17	1.07	2.24	7.72
Short-day, height 23 cm. Whole stem	.47	2.72	3.17	7.22
(Buds, flowers and small pods.)				
Plants 40 days old (2 + 38 days)				
Long-day, height 47 cm. Whole stem	1.27	2.20	3.47	10.82
Short-day, height 24 cm. Whole stem	1.35	6.25	7.60	13.60
(Buds, flowers and pods up to 4 cm.)				

* C-h refers to total carbohydrates or the sum of total sugars, starch and hemicelluloses.

While it would seem to be quite obvious that the initiation of reproductive organs is the function of some as yet unknown hormone(s) and not caused by the nutritional state of the plant, the carbohydrate-nitrogen re-

lationship concept should be mentioned here. It has been cited on many an occasion that a relative increase in carbohydrates over nitrogen in some sort of C-N relationship, causes a plant to shift from the vegetative to the reproductive state. This despite the fact that the proponents of the idea have failed to define what particular carbohydrates and what form of nitrogen have this specific dynamic function and what is really meant by the "relationship." For lack of a better procedure, data for determined carbohydrate and nitrogen compounds have been expressed by most investigators by way of ratios.

In the chemical analysis of the Biloxi soybean plants that had been grown under relatively short photoperiods and, therefore, made reproductive, the writer has expressed, for the stems, the various analyzed carbohydrate fractions, using hexose sugars as the basis, and total nitrogen, in the form of ratios. The results are presented in table 4.

An inspection of the records will show that at the age up to 12 days, when the photoperiodic induction was completed in the short-day plants, the carbohydrate-nitrogen ratio of the stems, at the nodes of which floral organs were initiated, was still *lower* in the short-day (reproductive) than the long-day (vegetative) plants. The difference undoubtedly was caused by reduced photosynthesis under the shortened photoperiod. Only beginning with the 20th day, when photoperiodic inhibition had manifested itself in the short-day plants, the Ch-N ratio began to increase, for now very much less food material was used for vegetative extension. Thence forward inhibition in stem elongation of the short-day reproductive plants became more or less permanent, carbohydrates accumulated rapidly and were stored chiefly in the form of starch. As a consequence, and in spite of some increase in nitrogen concentration also, the CH-N ratio for the stems of reproductive plants increased rapidly. It is quite clear then that *the initiation of sexual reproduction preceded the accumulation of carbohydrates and the increased Ch-N ratio.* Previous to the referred studies and since then much additional evidence has accumulated that carbohydrate-nitrogen changes in plants are not fundamental to flower initiation (Murneek, 21; Loehwing, 12, 13). Without considering any hypothetical "relationship," they are of significance, however, in connection with flower development and performance and the growth of fruit and seeds.

While considering the bearing of nutrition and metabolism to sexual reproduction, whether this be induced by the photoperiod or other environmental factors, one should be aware not only of growth inhibition, whether photoperiodic or otherwise (17, 18, 24), but also the recently disclosed periodic stimulation of growth, which seems to be associated with two phases of reproduction (Wittwer and Murneek, 33; Wittwer, 32). The first apparently occurs during synapsis (union of chromosomes) the second, and probably more effective one, during syngamy (union of nuclei at fertilization). By disbudding, defloration and defruiting experiments, Wittwer (32) has demonstrated that a period of renewed growth follows each of the above important phases of sexual reproduction. Two maxima in growth rate were observed following gametophyte and embryo inception. They were caused probably by the secretion of a special hormone(s) or plant growth substances during the two crucial phases of reproduction.

In consideration of nutrition of reproductive plants one should always bear in mind the fact that the reproductive organs, directly or indirectly, have a marked influence, both stimulating and retarding, on metabolism and vegetative development of the plant, which is often striking. This supplementary and in a way converse conception to the usually accepted idea that nutrition makes the plant develop in one direction or another is based on a considerable body of experimental evidence. It helps to explain more precisely metabolic changes and chemical composition of plants brought about as a result of photoperiodism and other environmental factors conducive to sexual reproduction.

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ANATOMICAL AND HISTOLOGICAL CHANGES IN RELATION TO VERNALIZATION AND PHOTOPERIODISM

by

R. H. Roberts *and* B. Esther Struckmeyer

University of Wisconsin

The cause of flowering in plants has been the subject of a rapidly increasing amount of literature in the past few decades. The majority of such papers have dealt with the environmental factors employed to induce blossoming rather than with any possible basic physiology of sexual reproduction. That is, such items of external environment as the degrees of temperature and quality or duration of the daily light have been more often the subject for investigation and emphasis than have the conditions which might consistently occur within the plant when blossom primordia are initiated.

The opposite effects which comparable applications of nitrogen have upon the blossoming and fruiting of apple trees which are in widely different stages of vigor directed attention toward the possibility of using histological conditions and anatomical characters as an index of the beginning of reproductive processes (16, 21). Observation of the photoperiodic effects and particularly the influence of temperature upon photoperiodism (27, 28, 30) increased interest in the question: Are there common physiological conditions present within plants and also common physiological reactions by different species of plants whenever sexual reproduction is initiated, even though uses of different temperature, light, water or nitrogen nutrient conditions are needed to bring about flowering?

Four different lines of evidence have been secured which indicate a common sequence of physiological events when blossom induction occurs: (*1*) The rhythm of CO_2 exchange was found to be unlike in flowering and non-flowering plants (24, 25). This was true of both long- and short-day plants. (*2*) The daily growth rate and diurnal cycle of growth change very quickly when plants are placed in conditions leading to blossom induction (11). (*3*) Root extension is greatly reduced when plants enter the reproductive state. That is, top-root ratios of a number of plants were found to be related to flowering of the plants and not to the day length used to induce blossoming (32). (*4*) A large number of varieties of plants, including day-neutral and long- and short-day types, and those with high or low temperature preference exhibited common anatomical characters when placed in an environment inducive to blossoming (32, 33, 36). A review and extension of these latter observations, together with a consideration of the available references to similar work and their significance to photoperiod and vernalization is the subject of this paper. A fifth physiological condition has recently been investigated (23). This is pigment content. It has been found that the fractions of chlorophyll, carotene, violaxanthin and xanthophyll present during the daytime as measured by the chromatographic method do not appear to be related to blossoming. Also, pigment conditions during the dark period are not consistently correlated to reproduction. It appears that the diurnal cycle of pigment content, especially carotene, varies with day length rather than with reproductive state.

Experimental Evidence: — Interest in the possibility of the anatomical structure of plant stems being associated with flowering arose from the

observations that sour cherry (*Prunus cerasus*) (17), plum (*Prunus nigra* Hort.) (19) and apple (*Malus malus*) (20, 21) have a greater stem diameter when blossom buds are formed. Later observations (38) on the time of apple blossom bud induction disclosed that the marked secondary thickening which is typical of "fruit" spurs is produced after blossom bud initiation has begun. The anatomical differences which are characteristic of non-flowering and flowering stems of the apple are like those previously found in annual and biennial plants (33, 37): "The flowering stems of all the species examined (at the fourth internode from the stem tip) seem to have certain anatomical characteristics in common, regardless of age or of photoperiodic classification. In contrast to the non-flowering stem, the flowering stem is characterized by: (*1*) a less active cambium; (*2*) a zone consisting mainly of thick-walled secondary xylem elements lying adjacent to the cambium in contrast to rather numerous vessels and thin-walled parenchymatous cells in the last formed xylem of the non-flowering stems; (*3*) generally thicker walls of the cells of the pericycle, perimedullary zone, and phloem; (*4*) freer staining with 'basic' dyes of the pericycle, perimedullary zone, and certain elements of the xylem."

Typical changes in the structure of the phloem as the reproductive state is entered were also found (33): "Some of the phloem characteristics which have been seen to accompany blossoming are: (*1*) Limited or slight formation of phloem cells following reduced cambial activity which precedes blossoming; (*2*) Small size of later formed cells; (*3*) Increase in cell wall thickness; (*4*) Increase in callose formation on sieve plates and fields; (*5*) Accumulation of inclusions in some cells; (*6*) Mechanical compression."

Additional observations upon the relation of cambial activity to the reproductive condition of some dicotyledonous plants (39) led to the following summary statements: "Vigorously vegetative plants have an active cambium throughout the length of their stems. The cessation or decrease of cambial activity which accompanies the production of flowers progresses from the region of the inflorescence toward the base of the plant, which it may or may not reach depending upon the degree of reproductiveness which the plant attains as measured by the relative number of primordia which differentiate as floral structures. If certain species of plants are allowed to reach an advanced stage of reproductiveness under favorable environmental conditions, the meristematic tissue of their stems tends to become entirely differentiated into xylem and phloem elements. This anatomical condition is a possible explanation of the death of such plants at the close of one reproductive cycle." Wilton had ample evidence to have proposed that the annual habit is due to a cession of cambial activity rather than to have only suggested this possibility.

Unpublished work upon the cambial condition in roots[1] has shown that the cambium becomes inactive or "lost" in maturing annual plants and fruiting biennials and that it persists in perennials and in those annual or biennial plants which have been kept in an environment which maintained them in a non-flowering state.

The relation of cambial activity and sexual reproduction has been

[1] Paul Bernstein, Lois Thomson Foster, Dr. B. E. Struckmeyer.

observed in all of 65 to 70 species of dicotyledons which have been examined.

The time and nature of the transition from the anatomical condition which is typical of non-flowering plants to that found in the flowering stems has been determined and described (34). A marked reduction in cambial activity and a corresponding increase in maturation of xylem and phloem elements was clearly apparent in stems of *Salvia splendens* var. Harbinger in 5 days after placing the plants in an environment inducive to flowering (short days and a warm night temperature). This is three to four days prior to the appearance of blossom primordia.

Different species exhibit different rates of reaction to an environment favorable to blossom induction. At optimum photoperiod and temperature, soybeans (*Glycine max* var. Biloxi, a short-day type) showed marked anatomical changes in five to six days and blossom primordia in nine to twelve days. *Xanthium echinatum*[2] responds more rapidly; anatomical changes were obvious in three days and blossom primordia were found in four to five days after the start of short photoperiod treatments. *Cosmos sulphureus* var. Klondike showed very distinct changes in anatomical structure after three short days and blossom primordia were observed in twelve days.

In the long-day species *Matthiola incana* (Stock, var. Christmas Pink) blossom primordia were found after 17 to 18 long light periods. Changes in anatomical characters were found in these plants after only five to six days of treatment.

From the preceding paragraphs it is evident that the first appearance of blossom primordia would not be an index of when induction begins. In fact, in the apple (38) and cranberry (31) induction has progressed to a stage where nearly complete defoliation will not interrupt it, as long as three to four weeks before primordia arise. This would seem to bring into question the desirability of dissecting the tips of plants to observe the appearance of primordia as is insisted upon by some workers. Changes in anatomical structure appear to correspond very closely to induction. Observation of this situation may be found to be useful if it is desired that the time of initiation be determined accurately.

The length of photoperiodic treatment needed sufficiently to induce a plant so that it becomes sexually reproductive even after being transferred to an environment inhibitory to induction also varies with the species or variety. Biloxi soybeans need approximately 17 short days (34) to establish effective "after-affects." It will be reported later that plants which flower terminally as *Salvia splendens* var. Harbinger will return to a vegetative type of growth even well after they are in flower if the plants are given long-day conditions. That is, they do not exhibit fixed after-affects.

It is reported (7) that *Xanthium* becomes sexually reproductive after only one long dark period (one short day) even though returned and continued in long days. Staminate flowers will usually but not always be produced by plants given one long dark period but in repeated trials it has

[2] From cultural comparisons and reactions to photoperiod this is quite obviously the same species as that used by Hamner and Bonner (7) and called *X. pennsylvanicum* by them.

been found that two or more long nights are necessary for the subsequent development of pistillate flowers.

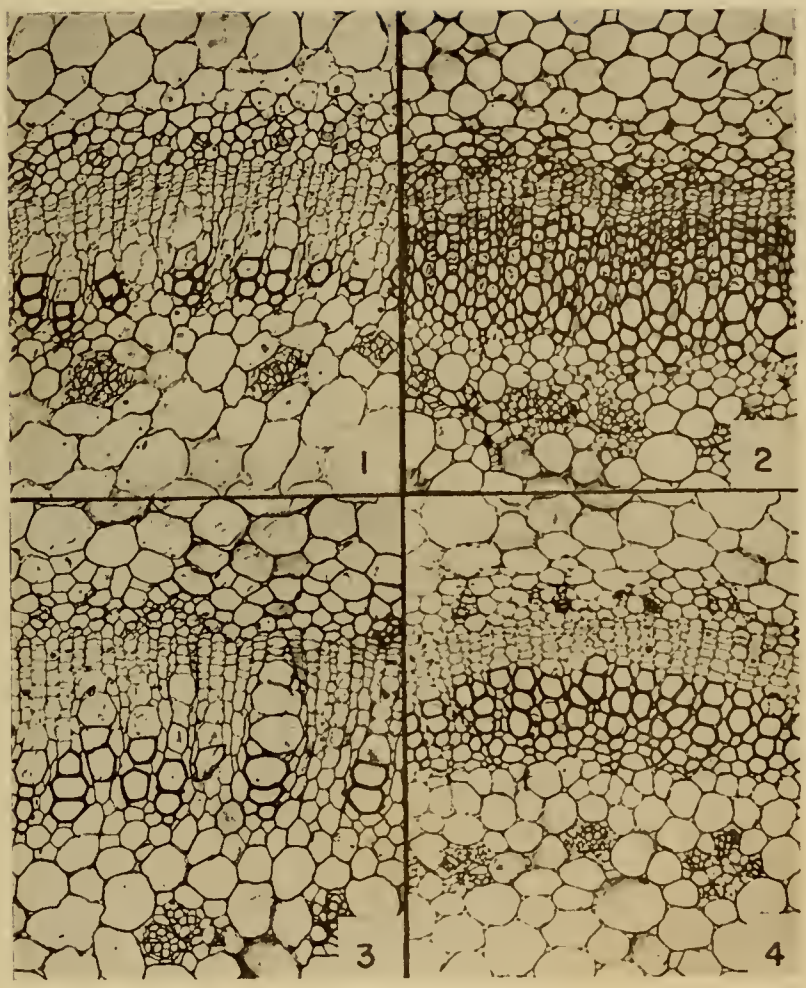
New Evidence: — Changes in anatomical structure have appeared consistently with or prior to blossom induction when usual conditions of environment are used. They have also been well in advance of blossom primordia. There remains the question of the anatomical history when blossoms are initiated under such unusual environmental treatments as reversed night temperatures (22), "temperature girdles," banding, and grafting (29).

When plants which come to flower early under relatively warm night temperatures as, *Cannabis sativa* (hemp), *Datura stramonium* (Jimpson weed), *Euphorbia pulcherrima* (poinsettia), *Glycine max* (soybean, var. Biloxi), *Nicotiana tabacum* (tobacco var. Maryland Mammoth), *Panicum milaceum* (millet), *Phaseolus vulgaris* (kidney bean), *Solanum capicastri* (ornamental pepper), *Xanthium echinatum* (cocklebur) and *Zea mays* (corn) are transferred to an environment with a warm (75°F) dark period of 13 hours and cool light period (55°F) of 11 hours, they soon become nearly etiolated or at least produce new growths with very little green color (23). Such plants are of particular interest from the standpoint of the physiology of sexual reproduction. They differentiate and develop blossoms and may even set fruits at almost the same rates as normally green plants in cool nights and warm days. Long continued development is not usual with such pale plants but the initiation of sexual reproduction is not inhibited and only slightly delayed by a lack of green color.

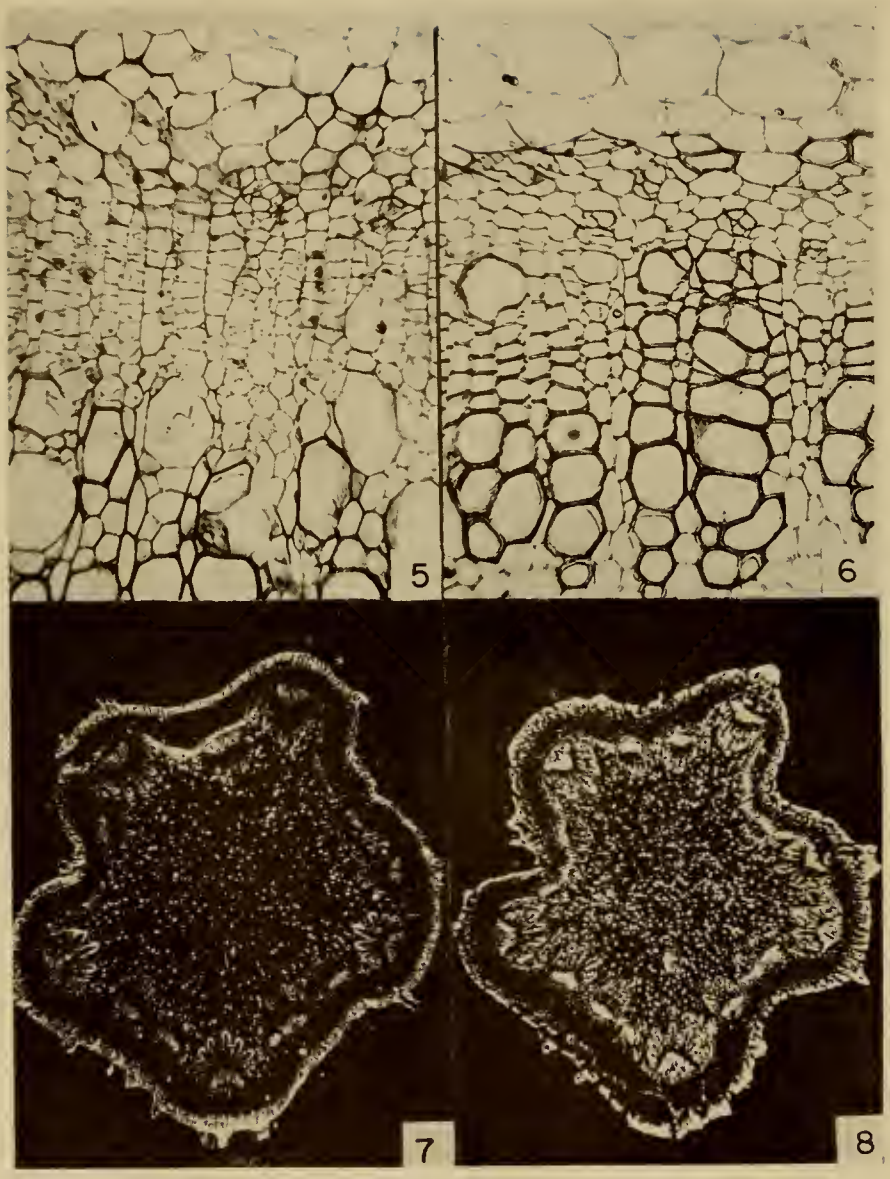
Examination of the stems of plants grown with warm nights and cool days discloses that they have an anatomical history parallel to those grown in cool night and warm day temperatures. While they have the thin-walled cells with slight inclusions which are typical of partly etiolated or shade-grown samples, reduced cambial activity preceded the appearance of primordia when the proper photoperiod was used to induce reproduction. (Figs. 1-4.)

Three unusual methods of inducing blossoming also resulted in plants with characteristic changes in cambial and cellular condition prior to and during blossom bud development. The short-day plants, poinsettia (*Euphorbia pulcherrima*) and Maryland Mammoth tobacco (*Nicotiana tabacum*) do not blossom in short days at warm night temperatures of 75°F (30). They will blossom in this environment if a current of cool air is passed through a short chamber placed about the stems some 3 to 4 nodes below the tips (29). The structure of the stems above the "temperature girdles" becomes typical of those induced to blossom by usual induction techniques (Figs. 5, 6). Borthwick, Parker and Heinze (2) report that cooling of the petiole of the leaf responsible for providing the flowering stimulus prevented the transfer of the stimulus and inhibited blossoming of Biloxi soybean.

Poinsettia plants in short days, but too warm at night to initiate blossom, can also be brought into blossom by wrapping taut rubber bands about the stems near the tips. When blossoming is induced in this manner, characteristic changes in the anatomical structure were found to occur above the point of banding.



FIGURES 1-4.—*Nicotiana tabacum* VAR. *Maryland Mammoth:* 1, Non-flowering plant in long photoperiods with cool nights and warm days. 2, Flowering plant in short photoperiods with cool nights and warm days. 3, Non-flowering plant in long photoperiods with warm nights and cool days. 4, Flowering plant in short photoperiods with warm nights and cool days. Cessation of cambial activity precedes blossoming.



FIGURES 5, 6.—CROSS-SECTION OF STEMS OF POINSETTIA (*Euphorbia pulcherrima*) : 5, Non-flowering stem. 6, Flowering stem sampled above a "temperature girdle" has a cambial condition typical of flowering stems.— FIGURES 7, 8.—Spodograms of *Xanthium:* 7, Ash residue of vegetative stem. 8, Same after five short photoperiods.

The induction of sexual reproduction by grafting a flowering plant upon a "receptor" plant has been reported by a number of workers (3[3], 7, 8, 10, 41). When plants are brought to flower by the grafting technique the receptor plants exhibit anatomical changes similar to those induced to blossom through photoperiodic conditions, temperature or age.

Two other lines of evidence show a correlation of anatomical structure with sexual reproduction. One is the characteristic amount of phloem tissue in a species and the other is the renewal of cambial activity when plants which are in flower are made to produce new vegetative shoots (34). Its significance is not known but it is very suggestive of a common physiological basis for sexual reproduction that several species of plants which blossom early and continuously in a very wide range of environmental conditions as buckwheat (*Fagopyrum esculentum*) were found to have a very limited amount of phloem tissue (37); also, that other species which can rarely be induced to form blossoms as commercial varieties of sweet potato (*Ipomoea batatas*) had a characteristically abundant formation of phloem.

The renewal of cambial activity after the induction period as in cases like the unilateral production of xylem cells resulting in the large-diameter spurs characteristic of the apple when blossom buds are developing, the growth of perennials after a rest period or the return to active cambial formation when plants are replaced in an environment unfavorable to blossom initiation (34) will not be considered now. Neither will a discussion of the questions arising in connection with late bud development, flowering, fruit set and fruiting be undertaken. Conditions most conducive to induction are of course often very different from those giving optimum fruiting in a commercial sense.

Literature: — There are rather numerous references to the effects of photoperiod or other external environmental factors upon stem anatomy (9). As the plants have been sampled according to the cultural treatment and not the reproductive state, it is not usually known but can only be guessed as to whether the anatomical condition observed bore a relation to blossom initiation. An example is HAMNER's statement (6, p. 586): ". . . . PSAREV *et al.* found an increased cambial activity during induction."

The papers by PSAREV (12, 13) and PSAREV and NEUMAN (14) which HAMNER cited do not record the cambial activity nor do they describe the cellular structure either during induction or at a later time. They report only an increase in stem diameter of mature soybean plants grown in short days (presumably due to longer continued cambial activity.) The short day plants of PSAREV (14) had some internodes which "assume a shape of abnormal swellings or 'tumors' which look like those induced by several different authors through treating the plants with growth substances." From this fact and also the statement that mature plants in short days averaged only 10.2 and 15.6 cm. in height, it appears that PSAREV was working with abnormal plants such as occur in short days in the greenhouse when the

[3] It is suggested that inexperienced workers take care to use correct temperatures when experimenting with *Hyoscyamus niger* as this plant appears more responsive to different levels of temperature than to long or short photoperiods.

nights are cold (55°F) and which also appear in the fields of the Midwestern United States of America as what farmers call "duds" (36).

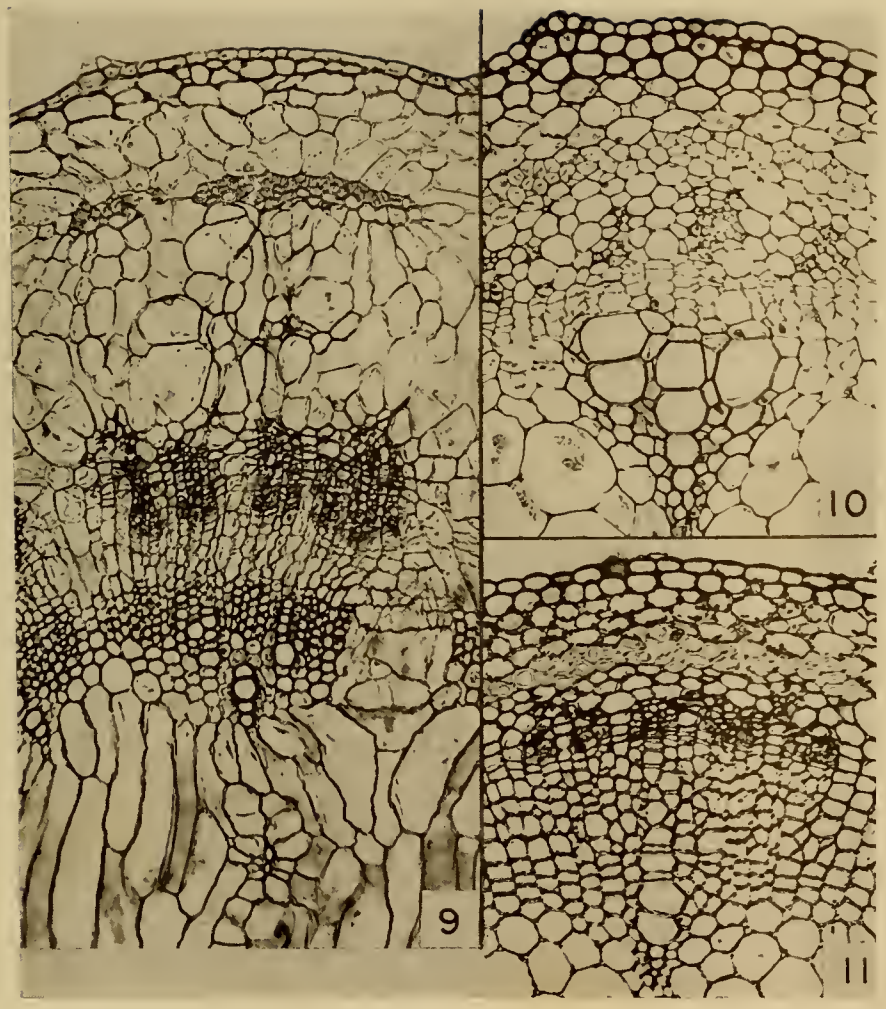
A detailed study of the anatomy of this type of plant shows definitely that the large diameter is due to increase in parenchyma cell size and not to increased xylem formation from cambial activity (Fig. 9). The thickness of these stems and presumably also of the short day plants of Psarev, is due to a combination of low temperature and short days and is not associated with induction. Plants which fruit normally in short days and warm night temperatures remain slender. Also, they have the anatomical conditions typical of reproductive plants (Figs. 10, 11). More evidence is needed on the relation of anatomical condition and reproduction. This should be secured by sampling and studying plants at the time of induction and early blossoming in comparison with actual non-flowering plants.

Withrow (40) has found an anatomical condition in non-flowering and flowering plants like that described by Wilton and by Struckmeyer. This consisted of reduced cambial activity and limited phloem formation in plants which flowered. This was found to be true of both long- or short-day plants and also occurred without regard to the nitrogen nutrition.

Plant Differences: — In the course of the induction of blossoming by numerous methods to ascertain the consistency of anatomical history of sexual reproduction, a particularly interesting difference in the reaction of plant species has been observed. We do not refer to the different or even opposite flowering responses of different species to like photoperiods or temperature treatments or age but to another plant characteristic which appears to have as much effect upon the type of experimental evidence which is secured as does the influence of certain external conditions. We refer to the blossoming habit: Plants which have only terminal blossoms react differently from those which have blossoms at numerous growing points along the stem; *i.e.* those which flower systemically (29). Thus Garner and Allard (5) showed there was no transfer of the flowering stimulus between branches of Klondyke cosmos (*Cosmos sulphureus*), a terminal flowering species. At much later dates morning glory (*Ipomoea purpurea* var. Heavenly Blue) (27), *Xanthium* (7), soybean (*Glycine max*) (1) and other plants with a systemic flowering habit were reported to show a transfer of the flowering stimulus.

This relation of terminal and systemic flowering habits to reaction to flowering stimulus from donor branches or leaves has been checked in only a few score of plants. It is anticipated that an exception to the general classification may be found. The nearest to it to date is *Perilla frutescens* (*nankinensis*). No transfer of the flowering stimulus with this systemic flowering plant has been secured in our trials even when the leaves are removed from the receptor branches. In the experience of some workers it is also necessary to keep the flowers removed from the donor portion. We have not tried this technique.

It is also interesting that plants flowering terminally are not induced to blossom by grafting the stem of a flowering plant onto a non-flowering one. (It would be interesting to know what the results of Moshkov (4, p. 230-1) would have been had he "decapitated" the receptor tobacco plants at a lower level, that is, in a region of the stem where blossoms do not ordinarily



FIGURES 9-11.—CROSS-SECTIONS OF STEMS OF BILOXI SOYBEAN: 9, Abnormally large and distorted parenchyma cells of "dud" plant grown in cool, short photoperiods (Magnification .52 times that of figures 10 and 11). 10, Non-flowering stem of young plant before induction. 11, Flowering stem of plant grown in warm, short photoperiods.

arise.) Several species which produce blossoms at any node have been readily induced to flower by the grafting technique.

The blossoming habit of the plant should be considered when "transfer" experiments are being planned. It should also prevent unjust criticisms being made such as have begun to appear in the literature, when two workers obtain different results, obviously from the use of plants of different flowering habits.

After-Affect: — Another phenomenon which varies with the flowering habit of the species is the difference in reaction to a change in environment, after the plant has come to flower. Plants with a terminal flowering habit as Klondyke cosmos, poinsettia, *Rudbeckia laciniata, Salvia* (var. Harbinger), stock (Christmas Pink) and Maryland Mammoth tobacco can be readily changed to a vegetative state after they have come to flower by placing them in an environment which inhibits flowering. Plants with a systemic flower forming habit as morning glory (var. Heavenly Blue), petunia (forcing), soybean (var. Biloxi), and *Xanthium echinatum* do not revert to a vegetative growth cycle in a reversed environment, once they have come to flower and fruit.

The continued flowering of an induced plant after being transferred to an environment unfavorable to flowering (provided it is of a species having a systemic blossoming habit) presents an interesting problem. The mechanism of the "after-affect" has been the subject of considerable theorizing. A possibility of an effective mechanism is presented by the fact that annual plants which show after-affects do not characteristically renew cambial activity once it has ceased at the time of induction and flowering (34). In this connection it must be kept in mind that plants which require a long period of treatment to establish a permanent after-affect will revert to a vegetative type and regenerate cambial activity if the induction treatment is discontinued before induction is completed. Terminally flowering varieties regenerate cambium whenever returned to an environment unfavorable to blossom induction.

Monocotyledons: — An extensive study of the relation of stem anatomy to flowering of monocotyledons has not been attempted as so few of the commonly available species have stems suitable for sampling when in a non-flowering state. The grains and grasses as well as most other locally grown species of this group are in an induced state before stems long enough for sampling of internodes are produced.

Histology: — Too little original work has been done on the question of the relation of plant composition to blossom induction to be of much significance. It is of interest that the etiolated type of plants grown in warm nights and cool days may have so little carbohydrate that no starch and almost no free reducing substance is found by qualitative tests.

Consistent differences in the mineral pattern of flowering and non-flowering stems have been found (35). It has also been repeatedly observed that a change in the mineral distribution becomes apparent very soon after plants are placed in an environment inducive to flowering. A changed pattern is evident in as short a time as two to three days in some species (Figs. 7, 8, opposite p. 95).

Like most of the anatomical studies reported in the literature, analytical studies have been more commonly on samples from different environmental treatments or of plants in later stages of flowering or fruiting rather than of samples in early stages of sexual reproduction (9). To secure evidence on the physiology of sexual regeneration, sampling of potentially flowering plants should be done at the time of blossom induction.

Similarly, cytological studies of the apical meristems involved in the differentiation of floral primordia are needed.

Role of Anatomy: — That no possible misunderstanding arise, it is clearly acknowledged that the significance of the anatomical situations which have been found to be associated with sexual reproduction is not known.

It is difficult, however, to avoid considering that the stopping of phloem formation at the time of induction and prior to blossom differentiation and flowering might not greatly affect transfer of the flowering stimulus as well as conduction of other elaborated substances from the leaves.[4] On the other hand, the evidence is not now sufficiently definite to justify proposing that anatomical conditions are causative in sexual reproduction, even though the possibility seems to exist.

Phytohormones: — The phytohormones have been considered as causal in blossom initiation by numerous workers (chapter 6, this series). At least, names have been proposed ("florigen" of ČAJLAHJAN and "anthesin" of CHOLODNY) for the as yet unextracted substance which is presumed to pass through a graft union and cause the flowering of a receptor plant. If phytohormones are the real stimulating agent they obviously work through the mechanism which inhibits cambial activity and induces maturation. This gives a clue as to the physiological reaction they would induce. A substance which would result in maturation phenomena would be unlike any commonly known phytohormone as the ones now available for plant treatments induce proliferation. Should a "maturity inducer" be isolated it should not only be of potential use in causing flowering but also be a possible remedy for cancerous growths, that is, if cancer is "the inability of cells to stop growing." Methods of extraction should be directed toward the securing of such a substance.

Relation with Photoperiodism: — Since anatomical conditions have been seen to be correlated with sexual reproduction, it is very obvious that a given photoperiod, as for example a short day, would not result in a common anatomical situation in different plants as it would either induce blossoming (of a short-day plant), inhibit blossoming (of a long-day plant), or have little if anything more than a time effect upon blossoming (of a day-neutral type).

[4] From our observations, a transfer of the stimulus-to-flower by grafts separated by a "diffusion contact" of lens paper (7) is not possible unless the proliferating tissue has penetrated the separating medium and made a direct contact between the donor and receptor stems as found by MOSHKOV (10) and by WITHROW and WITHROW (41). MOSHKOV reports a 10-day "physiological contact" is necessary to secure induction with *Perilla* grafts.

Relation with Vernalization: — A comparable situation exists in connection with any possible relation of vernalization and anatomical development. If vernalization be given a narrow definition, as a cold treatment, or if it be given a wide meaning, as any blossom-inducing treatment even including photoperiod as one item, it would not have a consistent relation with anatomy as no one factor of the external environment as moisture, nutrient, grafting, girdling, temperature, etc., have the same effect upon the inducing of sexual reproduction of different types of plants. Flowering is, however, correlated with anatomical development.

It would be interesting to know whether there are anatomical changes in the plants exhibiting devernalization comparable to those found in plants which do not have persisting after-affects (34).

Relation with Phasic Development: — The relation which has been found to be consistent between anatomical changes and the start of the cycle of sexual reproduction (blossom induction) should be a means by which to measure the general applicability of the proposition that the plant comes to flower by a series of phases, each of which must be completed before a succeeding one is entered.

Some interesting materials for study would be:

1. Pigweed (*Amaranthus retroflexus*) seedlings which flower with the first pair of leaves and even prior to the differentiation of secondary tissues, when grown in warm, short days.

2. The quick change from a non-flowering to a flowering state of *Xanthium* after two long-nights (staminate blossoms may be induced by only one long dark period).

3. Reversion to the vegetative condition of terminally flowering types of plants following a change of environment. (Rather spectacular examples can be produced with such plants as beets [*Beta vulgaris*] as the stems thicken into "beets" when the plants are transferred to an environment unfavorable to flowering.)

4. The continued flowering of plants with a systemic flowering habit after complete induction although having been moved into an environment unfavorable to induction.

5. Plants like *Nicandra physalodes* and buckwheat (*Fagopyrum esculentum*) which start to flower under very wide extremes of environmental condition and continue to grow and initiate and develop flowers even after maturing fruits are present on the plants.

It is suggested that observation of the anatomical conditions in the plant might be an aid in determining the boundary between the vegetative and reproductive phases. There is a relatively long lapse of time in many plants between the start of induction and the appearance of even microscopic blossom primordia. (Observation of the cambial condition in petioles can be made without greatly modifying a plant for later observation.)

Comment: — Use of the techniques of photoperiodic and vernalization experiments does not appear to offer solutions of the problem of sexual reproduction. The manipulation of external factors gives a record of the treatment needed to initiate sexual reproduction and thus serves as an aid in the control of plants for commercial or experimental purposes. An understanding of the physiological processes of reproduction would appear to depend upon a study of the internal factors and mechanisms involved

rather than upon an increase in knowledge of how to regulate the environment to induce flowering.

Anatomical changes in the stems (sampled at the fourth internode from the tip) have been observed to be consistently related to the entrance of a plant into the reproductive state. After-affects which are characteristic of some plants (with a systemic blossoming habit) and not typical of others (with a terminal blossoming habit) are associated with cambial activity. In fact, this difference in blossoming habits suggests a possible difference in the transport systems of different species.

A study of the relation of the anatomical development of a plant to sexual reproduction indicates that an item which is urgently needed for a solution of why plants blossom would be the extraction or discovery of a substance which would produce maturation phenomena when applied to or introduced into a non-blossoming plant, in contrast to the producing of proliferation phenomena by presently known phytohormones.

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LENGTH OF DAY IN THE CLIMATES OF PAST GEOLOGICAL ERAS AND ITS POSSIBLE EFFECTS UPON CHANGES IN PLANT LIFE

by

H. A. ALLARD

Formerly Senior Physiologist, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture

Introduction: — Only within comparatively recent years has length of day, as a factor of climate affecting the behaviors and natural distributions of plants, been given any emphasis. In all theories purporting to present the effects of the climatic complex upon plant life, even with reference to present conditions as well as to past geological eras, the temperature factor has always been given major consideration. The universally operative factor of daily light duration, in many respects equally as important as the temperature factor, has usually been entirely ignored.

Plant life in one form or another has existed upon the earth for many hundreds of millions of years. If length of day is a potent factor in affecting the various stages of development of plants growing at the present time, it is reasonable to believe that it has been effective throughout all past geological periods. So long as there is light, terrestrial rotation, inclination of the axis to the plane of the ecliptic, and revolution of the earth around the sun, cycles of length of day will continue to operate upon plant and animal life upon the earth.

Length of day must, therefore, always be a function of every climate. Geologists inform us that there have been great changes in world climate throughout all the great geological eras. Some climates have been characteristically warm and weakly zonal and others have been cool and strongly zonal. That there have been profound local, regional and even world-wide changes in climate involving length of day as well as temperature cannot be denied.

The astronomical relations responsible for earth climate are very complex and involve many factors including the earth's obliquity, the rate of rotation, the distance and eccentricity of the path of revolution around the sun, the length of time required to complete this revolution, as well as various conditions pertaining to the intensity of the solar energy and many physical conditions obtaining upon the earth itself. These astronomical relations of the earth and sun have engaged the attention of the most eminent astronomers and mathematicians. To attempt to determine the conditions of past geological climates and to learn the relations of these climates to the flora of any era on purely theoretical grounds seems a nearly hopeless task. Yet, if complete fossil records were obtainable so that the actual changes in the various geological floras could be properly evaluated, real material evidence would be at hand to supplement the astronomer's mathematical concepts.

It is a matter, then, of great importance to accumulate all available evidence relative to the changes that have taken place in the floras of past geological eras. As a matter of fact there is little other critical surviving proof that certain types of climate have existed in ancient geological periods, or that changes in the two great zonal controlling factors of climate, temperature and length of day have actually occurred and impressed themselves upon plant life. Whatever astronomical causes may have been responsible the character of the fossil remains of an ancient plant life more than any other evidence, may furnish the final proof that profound changes have taken place in the climate of a particular geological era. The astronomer, on purely mathematical grounds, may theorize about changes in the obliquity of the axis. However, were this obliquity actually to approach zero, with the same daily rotation that we have at present, caus-

ing a uniform length of day of 12 hours to prevail over all the earth, accompanied by weak zonations of temperature, there is every reason to believe that profound changes would take place in the floristic life-form and vegetation of the earth.

Various hypotheses have been advanced to explain the occurrence of warm and cool periods of climate, and the causes of the great Glacial periods. Some of these invoke astronomical changes as in the case of CROLL's (1875, 1889) semi-astronomical hypothesis, which makes use of both the inclination of the earth's axis to the plane of its orbit, and an increasing or decreasing eccentricity of this orbit. Others have invoked changes in the constituents and density of the earth's atmosphere, elevation of land areas known as the hypsometric Hypotheses, actual shifting of the Polar regions due to a thin crust sliding upon a semi-liquid nucleus (A. WEGENER, 1920; KÖPPEN, WLADIMIR PETER, and WEGENER, A., 1924), or changes in the localization of the permanent atmospheric lows and highs.

Reversals of deep-sea circulation causing the warmer waters to become deep-flowing currents moving toward the poles, while the cold water would flow equatorward, have also been suggested to account for climatic variations. It has been held that such reversal of the warm and cold ocean currents would explain the tropical and equatorial distribution of the Permo-carboniferous glaciation.

JOLY (1924) has put forward a theory that the earth's crust periodically warms and melts due to heat liberated by the transformations of radio-active elements. It is suggested that this blanketed-in heat would finally cause melting of the basaltic sub-crust, which would yield to various stresses and produce a period of marked crustal deformation or volcanic outflow. While it is generally recognized that the climate of the world has changed very profoundly many times, the causes of the changes are unknown, and no one theory appears wholly satisfactory in explaining all conditions.

While all of these theories assume that there would be changes in the temperature factor of the climatic complex, only two among these would at the same time involve accompanying changes in the length of day factor. In the one instance change of climate would be dependent upon changes in the inclination of the earth's axis and perhaps changes in the ellipticity of the earth's orbit, with possible changes in rate of revolution, rotation, etc. In the other instance, WEGENER's theory of crustal shifting involves changes in the geographical position of the poles. Such events could not occur without causing attendant changes in the daily light periodicity as well as in zonal temperature relations of large areas of the earth's surface.

The writer has given some consideration to certain angles of this problem in the light of a long study of the responses of plants to length of day. Since previous theories have completely overlooked the very important length-of-day aspects of climate, the recognition of this factor amounts to a new approach to the facts at hand and, for this reason, the present discussion has been prepared.

Ancient Climatic Cycles: — While geologists agree that great changes have occurred in the climate of the earth since the beginnings of life, the actual causes of these have never been determined. The character of the ancient climate can only be presumed by comparative studies of the material of the sedimentary rocks and the fossil remains which they contain. It is known that the plant life of the great geological eras has changed profoundly from time to time, and it is obvious that these changes must have been greatly influenced by shifts in climate due to changes in astronomical relations, crustal deformation or other causes.

At the present time the earth is nearest the sun in winter, since it is then in the perihelion portion of its orbit. Astronomers are of the opinion that this is not a constant relationship, and that in about 10,500 years it will be at the other extreme of its elliptical path, and reach its greatest distance from the sun known as the aphelion position. It would appear that these theories still assume that the inclination of the earth's axis will remain more or less as it is today. Astronomers make the claim that the mean value of the inclination of the earth's axis is progressively changing

to a measurable degree, but very slowly, so that after many thousands of years it will be reduced from a mean value of about 23° 27′ 3″, which is near its present inclination, to about 22½ degrees. After this it will again slowly increase its inclination. There are many conditions involved in these concepts, and it is doubtful if any categorical statements can be made as to actual happenings hundreds of thousands or even millions of years ago involving possible relations of position between earth and sun. It is obvious that even with all our geological evidence of the relatively very recent Ice Sheets, geologists have been unable to explain their occurrences with finality or to arrive at any agreement as to why a warm, even sub-tropical climate, devoid of marked zonal and seasonal differences such as prevail today, reigned over much or all the earth in Cretaceous times.

The earth has existed many hundreds of millions, or perhaps even billions of years since Cambrian time, and stupendous diastrophic events and profound cyclic changes in climate have occurred affecting the biological trends of life everywhere, but of the actual causes of these inconceivably ancient happenings there can be only supposition. It is possible that the inclination of the earth's axis has not always been as it is today, and that it has even been inclined to a greater or even to a much less degree than our present measurements show. An approach of the obliquity of the earth's axis to zero alone would bring about the most profound changes in the length-of-day aspect of climate and it is probable that new specializations and distributions of plant life would occur over all the earth. While pronounced zonations of climate at present obtain, geologists are of the opinion that weak zonations of climate have characterized certain geological eras. It is difficult to harmonize such conditions with a strongly tilted axis such as now prevails.

The Length-of-Day Factor of Climate and Plant Life:— The published results of GARNER and ALLARD in 1920 which for the first time showed that the flowering and fruiting of plants is intimately related to the length-of-day factor, has been amply substantiated by many other scientific workers throughout the world. It is now recognized that plants vary greatly in their responses to length of day. Some flower in response to shortening days, others require lengthening days or days of intermediate length, while a large group may be insensitive to length of day, or show a day-neutral behavior.

Plants of the short-day type, more especially those flowering in response to lengths of day near 12 hours, under our present terrestrial arrangements of zones and seasonal cycles, are of necessity confined to tropical regions or, if adapted only to the temperate zones, have become autumnal types. The latter flower in response to the shortened days which accompany the approach of autumn as do the native asters and goldenrods. The long-day plants are adapted only to the longer midsummer days, the duration of which increases with latitude until continuous day is experienced for varying periods at or near the poles. The day-neutral plants have no length-of-day limitations, since they can flower in response to all lengths of day prevailing from the equator where nearly constant daylight periods of 12 hours prevail, or even survive in high latitudes where very much longer days or

even continuous light may obtain. Their stature and habitus, however, may be greatly changed by particular lengths of day.

Plants with intermediate habits of response to length of day, flowering only when the days are neither too short or too long, would be confined entirely to temperate latitudes.

The prevalence of a 12-hour day over all the earth, with accompanying warm temperatures, would favor a poleward extension of the warmer zones with consequent changes in the distribution of tropical plant life. Moreover, this tropical length of day, at present localized in the middle zone of the earth, would favor the survival only of the day-neutral forms and such short-day forms as had become adapted to tropical short-day conditions of 12 hours, and to the short days of the autumnal season in high latitudes. On a purely length-of-day basis, all long-day plants which had become adapted to midsummer lengths of day exceeding 12 hours, or to the continuous day of the poles, would suffer extinction.

Anyone who has studied the narrow short-day requirements of the Poinsettia, *Euphorbia pulcherrima,* which flowers with great difficulty in response to lengths of day slightly longer than 12 to 12½ hours, can readily appreciate the profound changes which plant life as we know it today, would undergo should warm temperatures and a 12-hour day prevail over all the earth. Thousands of other woody and herbaceous plants with a behavior similar to that of the Poinsettia, other conditions being met, would find a means of ready invasion into high northern latitudes, one may presume even to the poles, under certain conditions. It may be stated that a constant length of day coupled with more or less uniformity of temperature conditions, would constitute the only climatic environment which would tend to distribute the same flora over all the earth.

Until the importance of the length-of-day factor was recognized as everywhere operative, in controlling the zonal and seasonal distributions of plant life, temperature control was regarded as the major expression of the climatic complex. There is no other factor of climate, however, that is so fixed and regularly cyclic as length of day. Even with a rigidly constant length of day of 12 hours prevailing over all the earth, such as a vertical axis or other condition would enforce, the temperature relations, even over a generally warm earth would show great local variations. These would be associated with differences in altitude and in cloudiness, differences dependent upon depth of the atmospheric envelope traversed by the sun's rays, and many other local effects that operate even at the present time. If zonal differences were evident these would be slight and weakly differentiated, and quite unlike the well marked zonal distributions associated with an inclined axis which gives us our seasonal climate today.

Although the Pleistocene Period was characterized by the development of great continental ice sheets thousands of feet thick in the northern hemisphere, a trend toward a seasonal climatic cycle had begun long before this. As a matter of fact some geologists have estimated that at least one million years have elapsed since the first Pleistocene glaciation. Whatever condition led to the great departures from the warm and widespread Cretaceous climate, glaciation was not necessarily a cause but a culmination following changes that had come about in terrestrial and solar relations.

The Cretaceous Flora: — Several hypotheses have been offered to explain the origins of our modern flora based upon the serious thought and patient investigations of various workers in many fields, including Geology and Paleobotany, Anatomy, Comparative Morphology, Ontogeny, Phylogeny and Phytogeography.

A great wealth of published material has been contributed by many students to the subject of the evolution of the Angiosperms, and the supposed origin of the great herbaceous group. Some of the most readable expositions among these discussions have been contributed by SINNOTT and BAILEY (1914), BERRY (1914 to 1924), BEWS (1916 to 1927) and many others, and the papers of these able workers in this field deserve special mention for their lucid and logical presentations.

The Cretaceous Period in the geological time scale is of the greatest interest to the paleobotanist, since it has afforded some of the most convincing evidence of the status of the ancient flora which preceded the great Tertiary transformations in plant life over all the earth. While all fossil evidence is fragmentary, nevertheless it must always hold an important place in all our concepts of evolution, and is rightly regarded one of the most direct sources of our evolutionary information.

The first recognizable remains of the flowering plants or Angiosperms have been found in the Cretaceous rocks. The appearance of these plants represents a biological event of first importance, culminating millions of years of struggle and evolution of this great phylum of life with all manner of crustal oscillations and climatic shiftings on sea and land. Plant life was abundant in other forms everywhere, and had maintained itself through eons of geological time preceding the Cretaceous Period but the flowering plants, it is conceded, were presumably very rare in the flora until the lower Cretaceous Period set in. There was then, seemingly, a very rapid evolution into the Angiospermous types over much of the world. While it is assumed that none of the modern species of plants had made their appearance in the Cretaceous Period, many of the recognized familiar genera of the present-day types had appeared, among these being *Acer, Platanus, Magnolia, Quercus, Juglans, Sassafras, Salix,* and many others. While the botanist sometimes speaks of these as simpler and more generalized types, they were probably merely different species in an early phylum called into expression and preserved by increased variations of the edaphic and climatic habitat.

All evidence that philosophical botanists have emphasized in forming their concepts of the evolution of plant life tends to favor the assumption that the early Angiospermous types were predominantly woody forms. The evidence for this concept is based in part upon the fossil material which is mainly of woody forms, and in part upon the observed present-day predominance of the woody life-forms in the tropical and subtropical regions of the earth. Large reptiles and subtropical plants appeared to have thrived in high latitudes in Cretaceous times, indicating mild or even subtropical temperatures over all the earth during this period. Because woody forms of plant life appear to have constituted the dominant life-form everywhere over a warm earth, as they do today in tropical and subtropical areas, this may be one of the reasons why the woody forms have been so extensively fossilized in the Cretaceous deposits.

The consensus of opinion of the leading Paleobotanists appears to be that the woody plants are the older of the two groups. However, one cannot be far wrong if he takes the more conservative view that both groups were in existence in Cretaceous times, but that the warmer and more uniform climate gave the former their high dominance as it does in the tropics and subtropics of the world today. It seems to be a well established fact that the woody Dicotyledonous Angiosperms at the present time are overwhelmingly predominant in the tropical flora, whereas in this class the herbaceous forms have preponderance in all the cooler regions of the world, more especially in the north temperate regions as well as in alpine and arctic lands everywhere.

It seems to be a somewhat dogmatic point of view to hold that the cold has somehow suddenly (speaking geologically) modified a woody stem, and reduced its structure by breaking the continuity of the woody ring into the many-bundled herbaceous type. There is probably no botanist who would hold dogmatically that herbaceous plants were non-existent in the Cretaceous flora or in that great interim of which there is no record, that must have prevailed between the laying down of the Cretaceous rocks and the deposition of the tertiary sediments.

It is not necessary to explain the actual origin of the woody or herbaceous elements of the ancient flora. It is enough for the present discussion merely to assume that herbaceous members existed in the Cretaceous Period, as most botanists would concede. Although the latter element may have been reduced to a very subordinate status under the warm conditions favoring woody forests, there is reason to believe that herbs were in existence in favorable though restricted habitats.

Evidence has been derived, also from other sources, one source deriving its conclusions from comparative studies of various families with ancient and modern representatives, and noting the relative abundance of the woody and the herbaceous life forms in these. In general the more ancient groups have a preponderance of woody types, while the more modern families contain the greatest number of herbaceous forms. While this evidence is not wholly acceptable to some students, others regard these comparisons as of some significance.

It is indicated, then, that the Cretaceous flora was becoming rapidly Angiospermous on a woody life form, and that this flora was of world-wide distribution, in response to a relatively warm and uniform climate prevailing over all the earth, even at the Poles. There was much intermingling of very unlike forms, involving types which are now dissociated and confined to distinct climatic and geographic zones. Palms and Poplars, Figs, Breadfruit, and Magnolias appear to have grown together for some unexplained reason, an association of species that is hard to visualize on the basis of our present climatic associations of such plants. However, if there was marked uniformity of climate over all the earth, sufficient to account for these striking interminglings and distributions of a warmth-demanding plant life, it is not illogical to assume that all the dominant factors of the climatic complex had undergone major modifications. It is fair to assume that a uniform length of day of about 12 hours may have accompanied this climatic expression, for such uniformity in daily light duration would become a potent factor in forming a widespread or even world-wide distribu-

tion of many species of plants that were not particularly sensitive to narrow ranges of temperature.

Changes in Plant Life in Tertiary Time: — Inferences regarding the climate of a given era or period must be drawn with great caution, yet leading authorities have come to more or less agreement on many points. It is considered by BERRY and others that certain features of the Cretaceous climate were quite unlike those of today, namely that the earth was much warmer, with much less seasonal change and zonal differentiation. These conclusions are drawn from various sources including the indistinct growth rings in the trees of this time, and the presence of a tropical and subtropical vegetation even in Greenland and in northern Alaska. In Eocene time which marks the earliest period of the Tertiary, conditions were very different from those which we experience today, although there is reason to believe that climatic and floral changes intensified in later periods of the Tertiary were being foreshadowed here.

Whereas in the Cretaceous Period, as previously stated, the Angiospermous forms showed an intermingling of what today appear to be tropical and temperate region species, even in the highest latitudes as revealed by fossil records, a progressive dissociation of these finally became evident, indicating a climate evolving into more strongly zonal distributions of temperature accompanied by changes in seasonal length of day. It seems remarkable that warm temperature conditions of this character could have prevailed in these high latitudes to sustain this type of flora here even in the Miocene, especially when only a little later in geological time great ice sheets had developed and covered these once warm regions. The tropical or subtropical types that had flourished in high latitudes gradually disappeared here, and an increasing number of deciduous forms made their appearance.

Pliocene plant life, as indicated by the fossil remains gave evidence of still more rigid sorting of the flora into tropical and temperate elements, which had begun in previous epochs so that tropical and subtropical plants were pushed even further southward toward their present equatorial limits. This separation of plant types appears to have proceeded more rapidly in North America than in Europe. These southerly colonizations of particular elements of the plant life that were formerly strangely commingled in far northern and now frigid regions have been interpreted as pointing to a gradual refrigeration of climate extending into lower latitudes, with consequent modification of the plants into new and specific adaptations by the changing climate.

It is not necessary to conclude that there was a progressive cooling of the entire earth's surface due to secular loss of heat from its mass. The evidence, on the contrary, points rather to some temporary climatic oscillation which may have resulted from events connected with the relations of the earth's axis to the plane of the ecliptic, to changes in the ellipticity of the earth's orbit, or to other unknown conditions. Whatever the cause it appears obvious that the world climate, formerly warm and uniform or approaching this condition in Cretaceous time, had become gradually differentiated into zonal distributions of heat and coolness, and this evolution continuing until the Pleistocene epoch, spread great ice sheets over the

northern hemisphere. These marked the culmination of the great climatic cycle of extreme refrigeration in northern latitudes.

The Tertiary Period is unique in that the plant life of the world radically changed its life form and distributions, if our geological evidence has been correctly interpreted. It has been shown that through the Cretaceous Period the woody forms of Angiosperms prevailed, and the herbaceous forms constituted a minor element of the flora so far as known. With the great world-wide climatic changes, which resulted in zonal distributions of temperature similar to present conditions, the herbaceous life form rapidly arose into prominence, and these Angiosperms, speaking in terms of geological time, soon dominated much of the world. That these events were associated with the Tertiary refrigerations of climate cannot well be doubted. The herbaceous plants, annual and perennial, proved to be more successful under the new climatic conditions. Many of the woody plants probably succumbed to the cold and other conditions, or were driven southward, but the herbs became the dominant life form, mainly in the north temperate regions, where formerly they appeared to have occupied a small niche in the world's flora.

Various theories have been advanced to explain the origin and dispersal of the great hordes of herbaceous Angiosperms which appeared in Tertiary time. As a result of this great change in floristics and life form the herbs by the infinite variety of their specializations and adaptations, not only became dominant in the Tertiary climate but have remained one of the most successful groups of plants in the present flora throughout the world.

Seasonal Cycles in Tertiary Climate and the Responses of Plant Life: — The exact astronomic conditions which were responsible for any of the great pan climates of former geological periods will probably never be known. Reasoning from the dependence of our present seasonal cycles upon an inclined axis, it can be assumed, however, that if there were no marked seasonal cycles in Cretaceous time, there were only slight variations in length of day. Since the present seasonal cycles with their accompanying changes in length of day, depend upon the obliquity of the earth's axis, it may not be unreasonable to assume that this axis which is now inclined nearly 23° 27′ 3″ had just begun to depart from a near zero obliquity in early Tertiary time. If this is a correct assumption a very gradual departure from the constant length of day of about 12 hours would have manifested itself in high latitudes in early Tertiary time. With increasing tilt of the axis progressively longer days would have obtained in higher latitudes and the equatorial regions alone would have retained the original short-day conditions of 12 hours as they do today.

The early Tertiary climate must have become progressively cooler, so that the warmth-demanding plants, formerly at home in Spitzbergen and Greenland, found inhospitable conditions here. These gradually would have given ground and perhaps have confined themselves only to tropical and subtropical regions which alone remained favorable to their existence, as it is at the present time for their descendants.

Those plants which were day-neutral, and great hosts of short-day plants, more especially those of annual behavior, together with hardy, perennial types, would have been able to exist and to multiply in high north-

ern latitudes. All these herbaceous plants would become an important group where formerly they were suppressed or occupied a minor place in competition with the larger and more vigorous trees and shrubs, as these less aggressive plants do today. It is obvious, then, that these cooler northern regions, more especially, because of the advances and retreats of the vast ice sheets here, became favorable land areas for the development of a great herbaceous Angiospermous flora. This appears to have been the final status of plant life in Tertiary time.

It is true that one must assume certain niceties of astronomic conditions, involving perhaps a vertical terrestrial axis, with a subsequent generation of wobble and obliquity of this axis, to develop season changes and even the glaciation stages themselves. This, however, seems no more unreasonable than many of the fanciful theories already promulgated to explain the great Glaciations of the Pleistocene Period, not one of which has been generally accepted as final by all geologists.

This hypothesis does not attempt to prove that herbs actually evolved from the great woody Angiospermous flora of the Cretaceous period by some direct response involving suppression or reduction of the continuous cambium elements of the stem with the production of intrafascicular parenchyma. It simply assumes that the herbs were already in existence at that time, but owing to the dominance of the woody forms, were in no position to compete with these, and, therefore, perhaps existed as a ground herbage for the most part in the great Angiospermous forests. Only the day-neutral and the short-day forms could have found the daily conditions of light duration favorable to their existence in Cretaceous time even under the most congenial habitat conditions if a 24-hour cycle prevailed with nearly equal durations of day and night.

This hypothesis appears to account for the great multiplication of Angiospermous herbs of the Tertiary Period, and their rise to subsequent numerical superiority in the temperate and colder regions of the earth as we find them, also, today.

It must be remembered that every geological cycle since the Cambrian Period has involved many millions of years, and incomprehensible periods of time have been required for each geological time period. While the geologist professes to speak in terms of years for the Triassic Period, the Jurassic, the Cretaceous or other periods, which have preserved their fossils for his studies, the gaps between these also probably represent many more millions of years of lost records. To measure conditions, then, of the earth's wobble and the inclinations of the axis at the present moment, and to hold that this has been always the actual condition even billions of years ago appears to be a rather dogmatic view which cannot but be regarded with suspicion.

It has been assumed that the herbs were already existent at the close of the Cretaceous Period, and there is reason to believe that herbaceous types of plant life are quite as ancient as the woody types. If it is true that the herbaceous type of plant is better adapted to cold climates, as its behavior indicates today, both in annual and in perennial forms, this life form must always have found favorable conditions for its existence even in past geological eras. Lofty mountains very early appeared on the great land areas

from the beginnings of the geological time scale as at present recognized, and such elevations have continued to appear through all the great geological eras. Even in a uniformly warm world climate such as is supposed to have characterized the Cretaceous Period, these high, cold mountain lands would have favored the development and preservation of the more adaptable herbaceous vegetation rather than the woody life form.

Subsequent Dispersal of the Tertiary Herbaceous Angiosperms: — Assuming that there has been a change from Cretaceous uniformities toward seasonal and zonal arrangements of warmth and cold in the Tertiary accompanied by inconstant seasonal lengths of day, it must naturally follow that the Angiospermous flora would be forced to undergo profound redistributions. The prominence of the woody life form would decline except in the warmer tropical and subtropical regions of the earth, and the herbaceous life form would assume a striking dominance in the colder Polar regions, and tend to follow the progressive extensions of these cold areas away from the Poles. Since the culmination of this new seasonal cycle appears to have brought glaciation only to the northern land areas, a series of events which occurred in the Pleistocene, the rise and spread of the herbaceous Angiospermous forms was especially favored in the northern hemisphere. However, similar changes of seasonal and zonal expression would also have prevailed in the southern hemisphere, and to the extent that continuity of the land masses allowed, the woody forms of plant life would also have been forced to recede toward the equator, followed by the rising tides of herbaceous plant life.

Students of plant distribution have assumed that the great northern herbaceous assemblages which appear to have arisen in the Tertiary, found a means of spreading even across the equatorial regions into the southern hemisphere far south of the equator.

It is reasonable to infer that some members of the northern herbaceous Angiosperms, in many instances, did find a means of dispersal into the lands of the southern hemisphere. However, it is possible to show that certain climatic barriers must have existed in Tertiary time to make this dispersion a naturally slow and a highly selective process. If in the Cretaceous Period, herbs also existed in these southern lands beside the dominant woody Angiosperms, as it is reasonable to suppose, these were less affected by the change toward seasonal progressions than were the northern herbs, for the reason that great ice sheets did not overrun these southern land areas during Pleistocene time.

The occurrence in the land areas of the southern hemisphere of a very large number of genera and species characteristic of the north temperate and even of the arctic zones has served to excite the comment of many botanists. Some botanists, have concluded that these elements could not have originated in the southern hemisphere, but must have found a means of migration into these areas from the great centers of distribution postulated as existing in the northern hemisphere.

The generation of similar climatic and seasonal cycles which must have taken place in southern as well as in northern latitudes, however, could have led to similarities of resemblance in the derivatives and their adaptations

evolving from the original endemic Cretaceous flora, if it has been correctly assumed that a world-wide distribution of related forms prevailed then.

While many northern herbaceous elements may have entered the southern hemisphere during Tertiary time, these plants would have found many climatic barriers in their way. It is true that great mountain ranges and high plateau lands afforded favorable altitudinal temperature zones which would assist the cold-demanding elements in crossing the heated tropical zones, but the factor of length of day seems not to have been considered in these speculations. It has been assumed that with the suppression of a dominant woody flora in cold mountain climates, the dispersal of the herbaceous element was an easy matter along these great natural highways.

It is true that in North America the great western Cordilleran highlands extended from Alaska through Central America to the southern tip of South America. If cool temperature alone were the only factor to be considered, a northern herbaceous element could readily have worked along these mountain highways across the hot equatorial regions, but it is not. The length-of-day factor of climate exerts a rigid control over the northward or southward distribution of many plants, and prevents their free dispersal and successful colonization into lower or higher latitudes. Length of day operates regardless of the temperature relations of the climatic habitat. The long-day plants which are of necessity confined to high latitudes having long days would be poorly equipped to traverse the short-day equatorial regions in spite of cold temperate or Alpine conditions on the mountain highlands. Presumably the day-neutral and the short-day types would find less difficulty in traversing the short-day equatorial regions into southern latitudes since they would be constitutionally adapted to these conditions. It would be otherwise with a very large class of herbaceous Angiosperms of long-day habit. These would find a suitable home only near their latitude of origin in the northern hemisphere, since favorable long days would exist nowhere except far south of the equator, and intervening conditions of unfavorable short days would militate against such migrations.

These climatic barriers would greatly restrict the dispersal of the northern herbaceous element into the ancient floras of Australia, New Zealand, Patagonia, South Africa and Madagascar. These limitations to the southward migration of important elements of the herbaceous Angiosperms which originated in the northern hemisphere, together with less refrigeration of the climate, and less continuous land areas for the ready migration of plants from other areas, may in part explain why the floras of the land areas of the southern hemisphere are not as rich in herbaceous elements as many of the floras of the northern hemisphere.

For these reasons one may reasonably question statements that a comparatively small body of herbs originated independently in Antarctic land areas, and that the seeming affinities of certain floras in the northern and southern hemispheres must be due to a great migration of northern herbaceous Angiosperms into these regions. It is possible that endemic specializations of a similar type of primitive flora arising in response to similar conditions could explain the presence of many of the genera and closely related species common to both the northern and the southern hemispheres.

The flora of the latter regions, then, would tend to display a greater percentage of shrubby elements than the northern floras, where extreme refrigeration caused greater extinction of the woody elements, giving room for a more abundant development and specialization in the surviving herbaceous elements. One may liken this hypothetical rise of the Tertiary herbs following the destruction of the woody Cretaceous Angiosperms to the noticeable inrush of herbaceous forms which follows the destruction of a great climax forest by lumbering and fire. Almost at once a host of adaptable weedy annual field forms are encouraged to colonize the denuded areas and to thrive as never before, until the perennial forms and the forests once more encroach upon this great temporary herbaceous assemblage.

To show the length-of-day difficulties which plants are forced to meet when suddenly transferred by man to regions where the length of day conditions are unfavorable, the common potato and its introduction into northern Europe where the summer days are very long, may be cited. According to VAN DE PLANK (1946) the common potato *Solanum tuberosum* could have been introduced from two sources. One group centering in Southern Chile where the summer days are long; the second assemblage centering in Colombia, Ecuador, Bolivia or Peru where the short tropical lengths of day near 12 hours prevail. From the experiences of growers in the high northern latitudes of Europe it would appear that the stock of the first European potatoes came from the short-day tropical source, since the plants did not tuberize well until very late in the season and continued to grow far into the autumn days or until killed by frost. This was a decided handicap, and it was recognized that great advantage would be gained if earlier sorts could be grown, in reality those better adapted to mature crops on longer days. Earlier strains have now been developed. From about 1573 up to about 1830, a period of about 260 years at least, late varieties or those maturing on short days were the only sorts grown in the British Isles and Europe. It is indicated that had the original stock been obtained from the long-day assemblage native to southern Chile, the problems of adaptation to European conditions would have been simpler, and earlier maturing sorts would have been available from the outset. These facts having to do with a conscious and very recent distribution by man illustrate some of the problems and difficulties plants must always meet in their natural disseminations and subsequent colonization in regions where summer lengths of day are not suited to their requirements. These short-day potatoes of the tropics not only could not have competed with the great forested assemblages of more northern latitudes, but were not adapted to the longer days of northern or southern latitudes. If at some past Cretaceous period the progenitors of the short-day potato assemblage had been able to invade more northern cool highland regions at a time when the days and nights were near 12 hours in length all over the earth, the strong zonal changes of climate in the Tertiary especially if associated with an increased length of day and intense refrigeration, would have driven the short-day assemblage into the tropics where we find this group at the present time.

Nothing at present appears to be known of the former distributions of the potato, north of the tropical regions. The writer is of the opinion that the short-day tropical group is the more ancient one, and that the long-day

assemblage in southern Chile represents a subsequent extension of range from this tropical group.

There is another characteristic of plants, which may be very intimately related to length of day, determining very largely their success in a given climate, namely, competitive ability. Long study by the writer dealing with a great variety of wild and cultivated plants has shown very forcibly that the competitive ability of many annual herbaceous plants depends upon a favorable length of day which will insure vigorous stature and abundant seed formation. In the case of many plants, more especially the short-day plants, which have adapted themselves to the shortening days of late summer and autumn in higher latitudes, this behavior deserves particular mention.

If low ragweed, *Ambrosia artemisiifolia,* Klondyke Cosmos, *Cosmos sulphureus,* or beggar-ticks, *Bidens bipinnata,* are grown from seed on short days of 10 or 12 hours from the outset, the reproductive phase begins at once, and extremely dwarfed plants, only two or three inches in height, will result, these flowering, fruiting and quickly dying in response to the short-day conditions. Such tiny plants often appear late in the season when the days have naturally shortened and may occur in far southern latitudes where the seasonal length of day is always much below the critical for flowering for many species. It is obvious that such dwarfed short-lived plants are poorly equipped to compete with rank and vigorous flora anywhere and more especially in those latitudes where the longest days of the season are below the critical for hastened flowering.

Such short-day plants find their greatest success in higher latitudes where a pre-vegetative period is favored by lengths of day above the critical for flowering. Under such conditions the plants, by their vigorous growth and increased stature, not only develop greater competitive ability in their native habitat, but produce enormous quantities of seed when the shortening days of late summer finally initiate the reproductive phase of development. Such short-day plants find their optimum development, then, not in those latitudes where too short-days prevail, as in the tropics, but in those latitudes where the reproductive phase follows a vigorous purely vegetative development which has been engendered by lengths of day in excess of that which initiates flowering. This type of response would manifest itself very promptly in a very large class of short-day plants, should conditions of climatic uniformity involving uniformity in length of day as well as conditions of warm temperatures, give way to marked seasonal and zonal differentiations which appear to have prevailed during Tertiary times. These changes would favor the seasonal multiplication and dominance of a very large class of typical short-day plants, characterized by low competitive ability in the tropics, but physiologically fitted to attain a very vigorous development in the middle latitudes, since here they would find a favorable seasonal schedule first for the pre-vegetative phase, then finally for the culminating reproductive phase. At the present time this is the normal life history of a great host of autumnal annual and perennial herbs in the higher latitudes, and this behavior represents a timely adjustment to our present marked seasonal and zonal length-of-day relations. It is obvious from these relations that a very large class of short-day plants

has probably been driven northward, rather than southward into equatorial regions, to find optimum conditions of survival.

Development of the Climbing Habit: — A large number of herbaceous and semi-herbaceous plants in both the tropics and in the warm temperate regions have become climbing forms. The suggestion has been made that these are herbaceous types because of the adoption of the vigorous climbing habit (SINNOTT and BAILEY, 1914, p. 594) but this concept appears to have little to recommend it as an explanation. The writer's studies of the length-of-day responses of a great variety of herbaceous plants indicate that the assumption of the dwarf bushy or the climbing habit in many instances is a direct response to particular lengths of day. Some plants have been induced to become climbers in response to short days, and others have shown the climbing behavior only when subjected to long days. Instances of these responses have been shown by members of different genera of the *Leguminosae,* including *Canavalia, Phaseolus vulgaris, P. lunatus, P. coccineus,* and the wild woodland bean, *P. polystachios* of eastern North America. Differences in the climbing response have been especially clearly shown in the case of the last named species, studies of which were reported by the writer (1938). This bean developed a low bushy habit of growth in response to constant lengths of day of 10, 12, 12½ and 13 hours. The climbing habit was not shown until lengths of day of 13½ hours or longer were experienced.

It is obvious, then, that if some great Tertiary transformation of climate had occurred that brought about marked changes in seasonal length of day giving the herbs an ascendency over all the cooler regions of the earth, and this event was followed by extensive migrations into all other favorable regions, the viney habit in many instances would also be called into response or in some instances repressed by this selective force alone of the climatic complex.

Length-of-Day Responses of the Woody Angiosperms: — Little mention has been made of the length-of-day responses of the woody plants in the present discussion. The annual herbaceous plants have usually been subjected to study by investigators because of the greater ease with which these in a short time can be grown to the flowering stage. The writer, however, in various publications has shown that the flowering of many of the woody plants is quite as responsive to length-of-day as the flowering of the herbaceous plants. This has been found true for a number of tropical and subtropical species, including Poinsettia, *Euphorbia pulcherrima,* Bougainvillea, *Bougainvillea glabra* and others. These two warmth-demanding plants are strictly short-day types, being able to flower only when the day length does not exceed 12 to 12½ hours. Such plants are of necessity confined to tropical regions not only because they find favorable warm temperatures here but because short days also constitute a feature of the climatic complex and make their existence possible.

Another tropical woody plant known as the Turkscap Hibiscus, *Malvaviscus conzattii,* is day-neutral in its behavior and flowers readily in response to long days (14½ to 15 hours) as well as to short days of 10 hours duration.

If, as the writer's theory postulates, a 12-hour day with warm temperatures finally became established over all the earth, all these plants could thrive as far poleward as temperature conditions would allow, and it is possible that therefore they may have thrived at the poles at the close of the Cretaceous Period. However, any change toward cooler conditions and longer days in high latitudes would have caused a quick recession of all these shrubs into the tropics. While the Poinsettia and the Bougainvillea would have been driven southward by the combined operation of two powerful climatic factors, namely, low temperatures and unfavorably long days, the Turkscap Hibiscus would have been brought to extinction only by the factor of cold, owing to its day-neutral constitution. Unquestionably there are thousands of other woody shrubs and even forest trees with similar narrow temperature and length-of-day characteristics, which rigidly confine them to tropical conditions of warmth and short days. These instances demonstrate how readily many species of a tropical flora growing over all the earth would suffer quick extinction were the climatic conditions of warmth and constant short days replaced by cold temperatures and long summer days in any geological period.

A number of shrubs, at present found in higher latitudes, appear to be adapted only to lengths of day in excess of the 12-hour photoperiods prevalent in equatorial regions. These are Althaea, *Hibiscus syriacus,* and Spice Bush, *Benzoin aestivale.* Tests have shown that neither of these shrubs was able to flower in regions where the length of day was permanently reduced to 12 hours. Such rigid limitations in length of day would confine these shrubs to regions and climatic zones where the summer length of day would exceed 12 hours, so far as sexual reproduction is concerned. Such forms of these species as have been studied would find no place in a climate characterized by a uniform 12-hour day.

In harmony with the present views of most geologists it is assumed that during the Cretaceous time, some combination of astronomic relations sustained a climate of marked uniformity characterized by warm temperatures and slight zonal differentiations over much of the earth. Such conditions of climate can hardly be postulated without assuming also an approach to a world-wide uniformity in length of day associated perhaps with a condition where the obliquity of the axis has approached zero over a great period of time. This position of the terrestrial axis with reference to the plane of its orbit would sustain a length of day from sunrise to sunset of about 12 hours over all the earth, with the exception perhaps of an extremely small area immediately around the Poles.[1]

Conclusions: — It is conceded by all students of ancient life that climate has always been a powerful factor in modifying the primitive vegetation. Temperature has been given the major role in the climatic complex in all theories purporting to explain secular changes in the primitive floras

[1] At the present time with the earth's axis inclined about 23° 27′ 3″ and in the perihelion portion of its orbit, the days and nights become nearly equal over all the earth, only at the time of the equinoxes about March 21 and September 21. Assuming a vertical axis, and the earth being an oblate spheroid, with flattening at the Poles, the rays of the sun always having a position vertical to the equator at noon would suffer their extreme refraction and shine upon the Poles although the sun might be actually below the horizon here.

of the great geological eras. Length-of-day, also always an interrelated condition of every climate, has never been recognized as specifically affecting the behaviors and distributions of plants. For this reason older theories have not been formulated upon a correct basis, and this has led the writer to develop a new hypothesis, making use of length of day as well as unfavorable temperature, in this approach.

It is assumed that beginning in Tertiary time, changes in these dominant conditions of climate made their appearance establishing marked seasonal cycles which naturally would be accompanied by lowering temperatures at or near the Polar areas, with attendant changes in length of day. While the length of day remained at or near 12 hours in the equatorial regions as before, the days poleward progressively increased in length as they do at present during the summer season, the longest days being experienced at the highest latitudes. These changes toward cooler temperatures and seasonal cycles became more accentuated in later Tertiary time, with continued accentuation into the Pleistocene, when great ice invasions occurred in the northern hemisphere.

It is not necessary to conclude that these ice ages followed as a direct result of a hypothetical change in the obliquity of the earth's axis and the establishment of marked seasons with variations in length of day, since these glaciations were confined to the northern hemisphere. However, these great glaciation occurrences are of particular significance since they favor the conclusion that a great herbaceous Angiospermous flora came rapidly into prominence, geologically speaking, in Tertiary time, and ultimately became dominant in the colder regions. Some world-wide change in climate appears to have favored this dominance and the subsequent dispersion of certain elements of this herbaceous flora over all the earth, if paleobotanists have correctly estimated the floral changes that actually occured at this time.

There has been no satisfactory explanation which will account for this major change from the Angiospermous woody life-form to the herbaceous life-form following changes in the relatively uniform climate of the Cretaceous Period, which appears to have favored the woody life form over all the earth. However, since the woody Angiosperms were dominant, and the herbaceous forms of these appeared to be an insignificant element of the vegetation, even in the Polar areas, there is reason to believe that weak zonal distributions of temperature obtained, and that a warm climate prevailed even in portions of the Polar regions.

While Sinnott and Bailey and others have advanced the hypothesis that the development of all herbaceous stems in the Tertiary Period resulted from a simple reduction in the amount of secondary wood chiefly, together with more or less increase of the ordinary parenchymatous tissue, it seems just as reasonable to assume that some herbs had long been in existence, playing a minor role in the great forests of woody forms in Cretaceous time. When the Tertiary Period brought about conditions unfavorable to these woody Angiosperms, the herbaceous Angiosperms, owing to their shorter life cycle, found better opportunities to increase and to adapt themselves to the new conditions involving cold seasons, longer days in summer, and sharp zonal distributions of warmth and cold.

It is assumed that the Tertiary change in climate interrupted the Cretaceous uniformities of warm temperature, weak zonal distinctions, and a world-wide uniformity of length of day, which had persisted at or near 12 hours in duration. With the establishment of long days in the Tertiary cycle, great numbers of woody plants flowering only in response to such short days became extinct, or were driven southward to find a home only in tropical regions where short days would still persist. On the other hand a great group of long-day plants that had been completely suppressed over all the earth during the Cretaceous Period by the world-wide prevalence of the short 12-hour day would now evolve in northern latitudes. While the long-day herbs would be confined to the higher latitudes the short-day Angiospermous herbs would readily adapt themselves to the seasonal summer cycle and flourish well toward the Poles becoming fall-flowering plants as at present. The day-neutral plants would thrive anywhere over the earth where habitat conditions favored their existence, whether the days were only 12 hours long as at the equator or where conditions of continuous light in summer would prevail, as at the Poles. Only day-neutral plants and long-day plants capable of flowering in response to continuous light would find Polar summers favorable to their existence.

Similar conditions of climate occurring also in the southern hemisphere involving seasonal changes causing colder temperatures and longer summer days intervening between the equinoxes would likewise induce the rise of an Angiospermous herbaceous element here. Owing to less rigorous conditions of cold, however, the original proportions of the woody Cretaceous flora would suffer less change, and a smaller assemblage of herbaceous Angiosperms would be called into expression.

It is known that in many instances the same genera and even the same species of plants occur in both hemispheres, and this has been explained by Sinnott and Bailey and others as due mainly to the dispersal of forms from the great northern reservoirs of herbaceous Angiosperms which arose to prominence in Tertiary time. These similarities in many instances may perhaps be in part explained by the assumption that they represent parallel lines of derivation descending from an ancient Cretaceous flora characterized by great similarity of forms the world over. Since the primitive assemblages were similar in Cretaceous time, and the conditions of climatic change in Tertiary time were of the same order in the higher latitudes, with respect to temperature and length of day, a certain degree of similarity should be expected in the descendants of the plant life of the two hemispheres.

The geographic dispersal of the Tertiary herbaceous Angiosperms from the higher latitudes where they first attained their dominance must have been influenced not only by the temperature factor but also by the length-of-day factor of climate.

The great equatorial regions with their permanence of high temperatures, their dominant climax forests of woody Angiosperms where high rainfall prevailed, and the permanently established short days, were powerful barriers to the dispersal into the southern hemisphere of many herbaceous Angiosperms. Even though there was a continuity of high mountain chains in western North and South America, which appeared to fur-

nish a convenient cool temperature bridge across the equatorial regions to mobile, migrating, herbaceous Angiospermous forms, because they afforded every degree of favorable temperature to the most selective and fastidious temperate region and boreal types, unfavorable length of day still remained always a permanent barrier to many plants even here. This was especially true for the long-day class of plants which had arisen in the temperate and polar regions of both hemispheres. The short-day and day-neutral plants were the only types which could have migrated freely northward and southward in both hemispheres. The eastward and westward dispersals would be limited only by the unfavorable temperature and moisture relations associated with high mountains, and by ocean barriers.

It is natural that in the warmer and more discontinuous land areas of the southern hemisphere, the primitive woody Cretaceous Angiosperms should have suffered less extinction and change, thus making conditions less favorable for the rise of the herbaceous Angiosperms. For unknown reasons these areas were less affected by cold than land areas in the high latitudes of the northern hemisphere, subjected to the great Ice invasions. Furthermore, there was less opportunity for the herbaceous descendants of this ancient flora to migrate elsewhere or for immigrant forms to enter these antipodean land areas from the reservoirs of the northern hemisphere. This may in part explain why, at the present time, there is great preponderance of the woody life forms in the southern hemisphere embracing many families and genera found also in the northern hemisphere. If the cold had been less severe with no marked differences in length-of-day the original Cretaceous woody Angiospermous flora would have changed less and a high degree of endemicity of woody forms would have been favored. For this reason this southern flora, long ago isolated by island conditions, and suffering less extinction of the more ancient forms, would have retained a more primitive facies even to the present day.

These considerations of the changes which took place in the Cretaceous flora followed by the rise of a great Angiospermous herbaceous flora more especially in high northern latitudes in Tertiary time are merely to be regarded as speculative in nature. The writer has put forward these hypotheses because they approach the problem from a new climatic angle, *length of day,* which hitherto has been an overlooked factor of the climatic complex affecting all plant life, past and present. If this factor is of such great importance at the present time exerting as it does a powerful selective action upon plants and confining these to certain climatic zones, then it is reasonable to assume that it has so operated in all the climates of the past.

No theory purporting to present the effects of ancient climates upon plant life can be taken too seriously which emphasizes the temperature factor only, and completely ignores the selective factor of length of day that also enters into every climatic complex. If palms, bananas, breadfruit, and other tropical plants which at present show definite limits of distribution formerly freely intermingled in high northern latitudes with a temperate region flora, these interminglings may not be entirely explainable on a temperature basis alone. One may assume conditions of uniformly warm climate, from the equator to the Poles which would bring many dissimilar types of warmth-demanding plants into a common association. However,

conditions of warmth could prevail either with great variations in length-of day, or be accompanied by conditions of a constant length of day such as now prevails only at or near the equator. The resultant effects upon the flora would be vastly different in the two instances. With no latitudinal differentiations in length of day, the two great controlling factors of climate, temperature and daily light duration, would work concomitantly toward a high floristic uniformity over all the earth, and no other combination of these major climatic conditions would operate so efficiently in promoting indiscriminate intermingling of dissimilar floristic elements everywhere.

There are few botanists today who have not been impressed with the length-of-day responses of plants. The recognition of this principle of plant response has led to a far greater interest in plant life, its behavior and distributions, than has perhaps ever been shown before, and a wealth of new information has accrued relating to the climatic relations both of our cultivated forms and of the wild forms everywhere.

It is thought that these speculations concerning the origins and the great changes which may have taken place in some of the ancient floras, will be of some interest to botanists, more especially since the hitherto unrecognized but powerfully operative factor of climate, length of day as a differential influence, has been given consideration.

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VERNALIZATION AND PHOTOPERIODISM IN THE TROPICS

by

S. M. Sircar

Department of Botany, University of Calcutta

Work on vernalization and photoperiodism in the tropics is comparatively recent. During the last decade numerous experiments on these phenomena were performed at several institutions in India and encouraging results obtained. The investigations carried on in the tropics up to the year 1935 failed to give any positive result and vernalization as an agronomic measure was considered to be of very little practical importance in Indian agriculture. This was largely due to the fact that systematic and sufficiently extensive work on developmental phases of tropical plants was not done. Later researches have shown a much wider scope for work on these phenomena in the tropics. Investigations done so far in India have mainly dealt with vernalization and photoperiodic response of crop plants under tropical conditions, while the physiological causes of these phenomena and the associated assimilation changes have been little studied. In a short discussion it is impossible to do more than give an outline to illustrate the main points in the researches on various Indian crops.

Rice (*Oryza sativa* L.) : — Following the announcement of the principles of phasic development of plants by Lysenko, experiments on vernalization by pre-sowing low temperature treatment of rice seeds were performed at several agricultural research stations in India with the object of escaping flood and other adverse conditions for growth and development of this plant. These experiments failed to show any change in the time and period of flowering; on the contrary in some varieties of rice a delaying effect of ear emergence was noted by S. M. Sircar (1945), and B. K. Kar and A. K. Adhikary (1945). The negative effect of low temperature on rice is in accordance with the natural condition of high temperature under which this crop grows in India. Throughout the life cycle of this plant, the average temperature requirement is from 20°C. to 37°C. and at no stage of its development does it benefit from a temperature below 15° C. P. Parija and K. P. Pillay (1944) have however noted that pre-sowing low temperature and anaerobiosis treatments induce flood resistance in some varieties of rice. The influence of high temperature on acceleration of flowering has been shown in a number of varieties of rice by P. Parija (1943), S. Hedayetullah and N. K. Sen (1941), B. K. Kar and A. K. Adhikary (1945), and S. Hedayetullah and B. N. Ghosh (1946). P. Parija has observed that pre-sowing high temperature treatment, in addition to acceleration of flowering, results in better resistance to drought conditions. The results of their work indicate that rice has a vernalization stage of high temperature. The response is of varietal character, but it remains to be seen how far these variations are due to different reactions of varieties to day length.

According to the time of harvest there are two main crops of rice in India, *viz.*, summer and winter crops. Flowering of summer varieties

takes place when seasonal day length is above 12 hours and winter varieties flower at day length less than 12 hours. Thus the time of flowering due to variation in day length as the basis of classification of paddy varieties was known before the principles of photoperiodism were announced by GARNER and ALLARD. The influence of different day length on flowering has been studied by M. ALAM (1940-41), S. M. SIRCAR (1942, 1944, 1946), S. M. SIRCAR and B. PARIJA (1945), B. K. KAR and A. K. ADHIKARY (1945), A. B. SARAN (1945) and J. C. SENGUPTA and N. K. SEN (1944*a*, 1945). B. K. KAR and A. K. ADHIKARY (1945) have reported that winter varieties which do not respond to high temperature treatment show earliness when given short-day treatment. These results indicate that short days are essential for flowering of winter rice. But the delaying effect of pre-sowing low temperature on ear emergence persists even after short day exposure of seedlings, for S. M. SIRCAR (1945) and J. C. SENGUPTA and N. K. SEN (1944*a*) have shown delay in the onset of flowering of some varieties of paddy by pre-sowing low temperature followed by short day treatment of seedlings. J. C. SENGUPTA and N. K. SEN (1945) have observed that when winter varieties are sown late in September (when the plants are normally exposed to photoperiods of less than 12 hours) 16 hours day length in the seedling stage for one month tend to induce early flowering. On the other hand the work of A. B. SARAN (1945) shows that long days are detrimental for growth and flowering of winter varieties. It is interesting to note that in summer varieties short day treatment delays flowering and also annuls the earliness by high temperature treatment (S. M. SIRCAR and B. N. GHOSH, 1947).

Vernalization by high temperature as an agronomic method has obvious difficulties. The germinating seeds when exposed to high temperature vernalization rapidly grow into seedlings, involving difficulties of transportation, and these seedlings are often attacked by fungus. On the basis of short day requirement of paddy varieties a method of vernalization by the application of short days to seedlings for varying periods has been suggested by S. M. SIRCAR (1944). The method has been found to be effective in transplanting varieties of rice, since the process of supplying short days by cutting off the excess sunlight in seed beds does not entail practical difficulty to rice growers. Vernalization response varied according to the nature of a variety; in a winter variety, *Bhasamanik,* earliness with increased grain yield has been noted. The increase in grain yield is associated with an increase in the number of ear-bearing tillers. Under normal conditions all the tillers of a rice plant do not survive to maturity, while later formed ones die away without forming ears, but an exposure of seedlings to effective photoperiods resulted in almost all the tillers bearing ears (S. M. SIRCAR, 1946). The vernalizing effect of short days is of a quantitative nature as the degree of earliness increases with the duration of the treatment. A remarkable influence of short days on the reduction of flowering duration from 133 to 47 days has been noted by S. M. SIRCAR and B. PARIJA (1945) in a winter variety, *Rupsail* (Plate 11). The flowering of rice within such a short period has not been reported previously as J. M. HECTOR (1936) and M. ALAM (1940-41) have noted that the minimum flowering duration of rice is 60 days. The effect of short days on the acceleration of flowering in

FLOWERING IN A WINTER VARIETY OF RICE (Rupsail).

this variety is reflected in the curtailment of vegetative growth of the main shoot, which bears 10 leaves as against 16 in the control. It is interesting to note that such a reduction in the flowering duration has only been noticed in the main shoot which received the photoperiodic exposure, while in the first and second tillers flowering was progressively delayed and in the remaining tillers ear emergence was at about the same time as in the control tillers. On the basis of the hormonal theory of development (K. C. Hamner and J. Bonner, 1938, M. H. Čaĭlahjan, 1936) an explanation for the variation in the flowering times of the main shoot and tillers is suggested. It appears that the flowering behaviour of the main shoot and tillers is related to the distribution of flower-forming hormone in the growing points. Hormone synthesized in the leaves exposed to short days was first translocated to the growing point of the main shoot and induced flowering; in addition, a portion of it accumulated at the growing points of the buds formed at the time of photoperiodic exposure. When these buds grew into tillers, accumulated hormone caused their flowering, while the tiller buds formed after the period of exposure received very little of the hormone, and consequently their flowering was as late as the control. Thus it seems that the distribution and concentration of flowering hormone, florigen, could be the cause of the variation in the flowering of the main shoot and tillers of the winter paddy, *Rupsail*. The whole question requires further investigation on the nature of the growing point at the time of photoperiodic exposure.

In recent years the classification of plants into short and long day types has been questioned by R. O. Whyte and M. A. Oljhovikov (1939) as investigations on wheat, millet, rye and other cereals have shown that short day or dark requirements of plants is inherent in the so-called short day plants not throughout their life time but only during a definite period of their development. After this period is completed short days tend to retard subsequent development and long days are required. Accordingly R. O. Whyte and M. A. Oljhovikov have concluded that so-called short day plants are not typical short day plants but may be described as short day → long day plants. In winter rice a different picture is obtained (S. M. Sircar, 1946). The acceleration of earing is maximum and grain yield increased when *Bhasamanik* seedlings are exposed all through to short days and there is no succession of short and long days. Earing in the main shoot of *Rupsail* is completed during short-day exposure for 6 weeks. After this period long day treatment is found to retard flowering in the tillers for which short days are necessary (S. K. Mukherjee, 1946). These results indicate that winter rice completes its developmental phases under short day conditions and is a typical short day plant.

Wheat (*Triticum vulgare* Vill.) : — Failure of vernalization response to pre-sowing low temperature treatment of early varieties of wheat was noted by B. K. Kar (1940, 1942-43), and B. P. Pal and G. S. Murty (1941), while B. Sen (1943-44) observed earliness in several late varieties from North Western India. Although low temperature treatment failed to induce earliness in B. K. Kar's experiments (1942-43), the treatment was effective in inducing an increase in chlorophyll development of the leaves of young seedlings, a greater output of tillers, a higher percentage of culm to tiller and a greater flush of ear emergence. According to him, failure of low tem-

perature treatment to accelerate flowering is due to the prevailing environmental conditions, of which short day-length is an important factor. Exposure to short-days in these strains was found to prolong, and long days or continuous illumination to curtail, the vegetative period. An exposure of low temperature treated seeds to long days for a period of only 7 days induced a significant earliness in the varieties which all along the rest of their life cycle were grown under short day conditions. B. P. Pal and G. S. Murty (1941) have also shown acceleration by long photoperiods and retardation by short days. It thus appears that for vernalization of wheat in India a photostage of long days is necessary, and once this is passed the plants complete their developmental phases independent of subsequent day length. Wheat being a winter crop, its low temperature requirement under Indian conditions is met by sowing in winter, but the prevailing short day length delays the completion of the photostage till the natural day length increases, when flowering takes place. Comparing the results of simultaneous sowings of the same varieties at Delhi (Lat. 28.38° N.) and Almora (Lat. 29.37°N.) in October and February, B. Sen (1943-44) considered that after-sowing environmental factors completely mask the effect of chilling of seeds. It would be interesting to find out in these cases the effects of different photoperiods on the strains showing acceleration of flowering by chilling.

K. K. Nanda and J. J. Chinoy (1945), in an attempt to prove the presence of a developmental phase associated with the formation of normally functioning gametes, have shown that long photoperiods as well as short photoperiods after the completion of the photostage increase pollen sterility, while with natural day length sterility is very much lower. This emphasises the importance of a critical number of long days, beyond which long days have only an adverse effect. According to B. P. Pal and G. S. Murty (1941), varieties of English wheat grown under tropical conditions require chilling followed by long days for inducing earliness; in the absence of chilling long days have no effect. For Indian wheat, on the other hand, chilling is not as important as long days for vernalization. But for yield and normal growth low temperature is an essential feature, as in summer sowings the crop yield becomes poor. They have further shown that the flowering duration of Indian wheat despite the prevailing short day condition is less than the English wheat grown under identical conditions. These differences in the behaviour of the varieties of English and Indian wheat support the thesis of N. I. Vavilov (1941) that by centuries of adaptation in tropical climate these strains have become differentiated into a distinct ecological and physiological group.

Mustard (*Brassica* spp.) : — Acceleration of flowering by pre-sowing low temperature treatment of sprouted and unsplit seeds of the Indian varieties of mustard was noted by B. Sen and S. C. Chakravarty (1938, 1942). Response was more in the case of sprouted seeds than unsplit seeds. Although the degree of vernalization induced is less in the unsplit seeds its advantages are: (*1*) germination of almost all the seeds, whilst sprouted seeds germinated only 30 to 40 per cent, (*2*) retaining power of germination without devernalization when dried and stored at room temperature for more than six years (B. Sen and S. C. Chakravarty, 1946). The effects

of drying and exposing vernalized seeds of mustard to high temperature were found to be different from those of wheat (M. Lojkin, 1936) and winter rye (F. G. Gregory and O. N. Purvis, 1938) where such treatment results in devernalization. According to B. Sen and S. C. Chakravarty (1942) the different effects of heat treatment are not due to the types of embryo concerned but to the stages of the development of the seed during the period of low temperature treatment. F. G. Gregory and O. N. Purvis (1938) have reported that devernalization takes place when vernalized winter rye seeds are exposed to high temperature, but there is no devernalization when the embryo developing in the ear is chilled. The effects of drying on the vernalized embryo at the preceding and succeeding stages of dormancy are thus different. The stage of the development of the mustard embryo lying within the elastic limit of the seed coat at the time of low temperature exposure was compared with that of the developing embryo of winter rye chilled in the ear. Although low temperature does have a quantitative effect on vernalization of mustard, yet low temperature is not obligatory for flowering, because in sowings in summer the time to flowering is very much reduced without pre-sowing low temperature treatment (B. Sen and S. C. Chakravarty, 1942). In their experiments on photoperiodic response they have observed that mustard type 27 is neither a short day nor a long day plant since it flowers under photoperiods of 10 hours as well as of 16 hours. But it is not indifferent to photoperiods, as flowering can also be induced earlier by subjecting the seedlings to increased photoperiods without chilling. They have indicated the importance of prevailing temperature during photoperiodic exposure; with higher temperature range the same photoperiod causes a greater shortening of the vegetative phase.

J. C. Sengupta and N. K. Sen (1944*c*) in their studies on the effect of the time of sowing of mustard have made contradictory statements, *i.e.*, that the vegetative period shortens with low temperature; further they mention that the same variety shows a lengthening of vegetative period with the shortening of the light period and a greater shortening of vegetative period is observed with increased temperature range. These statements have been criticised by B. Sen and S. C. Chakravarty (1944) as they have found, under otherwise similar cultural conditions, that lower temperature invariably lengthens the vegetative period. J. C. Sengupta and N. K. Sen (1944*c*) failed to show acceleration of flowering by low temperature treatment of two varieties of mustard. This may be a case of varietal difference and according to B. Sen and S. C. Chakravarty (1944) the period of low temperature of 30 days in their experiments is too short a period to induce vernalization.

Miscellaneous Crops: — *Gram* (*Cicer arietinum* L.) — Vernalization response in gram was noted by B. P. Pal and G. S. Murty (1941) and K. P. Pillay (1944) although I. M. Vasiliev (1939) classed gram among those plants which did not respond to vernalization treatment. The importance of low temperature in the phasic development of this crop has been suggested by B. P. Pal and G. S. Murty (1941) from complete failure of unvernalized plants to form even flower buds under natural days in summer. Varieties with long life periods respond more than those with shorter

duration. Long photoperiods are also found to bring about earlier flowering and short photoperiods tend to retard flowering. Combination of low temperature and long days still further accelerates flowering. Like mustard, vernalized seeds of gram undergo no devernalizing effect when such seeds are stored for more than 3 months or subjected to high temperature (B. P. Pal and S. Ramanujam, 1944). But exposure of seeds to low temperature and high temperature alternately does not produce vernalization. It has further been shown that seeds could also be vernalized during the time of ripening on the plant by low temperature treatment.

Jute (*Corchorus capsularis* L. and *C. olitorius* L.).—For the production of fibre from jute, acceleration of flowering is of no practical importance, but formation of early seeds has obvious advantages for breeding more generations in one year and this has been claimed by J. C. Sengupta and N. K. Sen (1944*b*), and B. K. Kar (1944) in their studies on photoperiodic effect on jute. Short day exposure reduced the fruiting days from 135 to 36 days with a possibility of growing more generations in the same season (J. C. Sengupta and N. K. Sen, 1944*b*). On the other hand long photoperiods were found to delay flowering.

Cotton (*Gossypium* spp.) — Pre-sowing temperature treatments on cotton seeds have little effect but short days produce early flowering (B. Sen, 1944-45).

Sugarcane (*Saccharum officinarum* L.). — By varying day length the flowering of sugarcane varieties has been controlled by N. D. Yusuff and N. L. Dutt (1945). It is interesting to note that short days of 2 hours induce flowering in wild forms (*Saccharum spontaneum* L.) which do not normally flower at Coimbatore (Lat. 11.0° N.). Long days are found to delay flowering in the cultivated varieties. By controlling light periods flowering of late and early strains of cultivated and wild *Saccharum* spp. has been so adjusted that a wide crossing is possible.

Soy bean (*Glycine hispida* Maxim.) — No appreciable effects of different temperatures on the flowering of Soy bean were found by B. P. Pal and G. S. Murty (1941). However, a remarkable effect of diminished photoperiod of 9.5 hours on the acceleration of flowering with improved quality of beans has been recorded by B. Sen (1944-45).

Biochemical Changes in Relation to Vernalization and Photoperiodism in the Tropics: — Comparing the enzyme contents of vernalized and unvernalized seeds B. Sen (1943-44, 1944-45) found that diastase and phosphatase in wheat; lipase, catalase and phosphatase in mustard and diastase in barley are higher in the vernalized seeds. In order to understand fully the effects of photoperiods on the acceleration of flowering and growth rate of rice culminating in increased grain yield, investigations on the assimilation changes of the plants subjected to different treatments were carried out by S. M. Sircar and his students, the approach to the problems being different from that of previous workers in this field. Photoperiods necessary for the acceleration of flowering of winter rice were applied in the seed bed, and after transplantation the chemical composition of the plants was determined at frequent intervals, with a view to ascertaining the differences in metabolites caused by the photoperiodic induction. The work on carbohydrate metabolism (S. M. Sircar and P. M. Samantaray, 1942) showed

that short day treatment increases the dry weight of the plant, and the earlier leaves at the end of the daily photoperiod show a greater accumulation of total sugars than the control while there is a decreased sugar content in the later leaves. The accumulation of sugar in the earlier leaves was found to be associated with more production of tillers at these stages, while a fall of sugar content in the leaves of later stages was related to the translocation of sugars to the developing ears. It thus appears that the reduction in day length from normal daylight of about 13 to 10 or 8 hours has not reduced the photosynthate formed; on the contrary, suitable photoperiods stimulate the plants to the production of increased dry matter. It was observed by S. M. Sircar and B. N. De (1947) that the nitrogen metabolism of rice plants is greatly influenced by 10 hours photoperiod in the seed bed and these effects are noticeable throughout the life history of the plant. Absorption of nitrogen is greatly increased in these plants and a part of it is metabolised to protein. The increase in nitrogen content occurs in conjunction with increase in growth rate. It is interesting to note that at the growing apex of the short day plant, where flower initials have been laid down, a large accumulation of amino acids takes place. How far the accumulation of amino acids and their nature are related to the initiation of flowering is an interesting problem for further investigation.

General Considerations: — The results presented in the foregoing pages clearly indicate the influence of day length on the flowering of tropical plants and refute the view expressed by W. W. Garner and H. A. Allard in their first communication (1920) that small changes in natural day length of the tropics do not produce any photoperiodic effect on the plants. The facts that winter varieties of rice flower only when day length shortens, and that short day length accelerates flowering without adverse effects on growth, are ample evidence for the existence of short day requirements in these varieties. In other varieties of rice the influence of day length is less marked; they are not responsive to short days and flower at day length more than 12 hours but without any acceleration after exposure to long days. An interaction between short day and high temperature in the phasic development of plants is exhibited in tropical crops, except in the cold weather crops like wheat, mustard and gram where there are indications of relationship between low temperature and long day. High temperature and short days are obligatory factors for winter rice, while the absence of low temperature effect on the flowering of Indian wheat or of mustard in both low and high temperatures and in short and long days shows that such an obligatory relationship between low temperature and long day does not exist. It appears that by centuries of adaptation in tropical climates these plants have lost the significance of low temperature in the transition from vegetative to reproductive phase, although its influence on vegetative growth persists. Assimilation changes induced in the rice plant by short day exposure of the seedlings indicate that with the photoperiodic perception in the seedling condition metabolic activities are stimulated, resulting in the formation of an unknown substance or substances which on transmission to the growing point participate in flowering.

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Postscript:— Vernalization by high temperature has practical difficulties. Radicles and plumules emerge from the seed coat during treatment involving difficulties of transportation and broadcast sowing. This has been overcome in two varieties of summer rice by limiting the moisture content of seeds to 25 to 30 percent of fresh weight. Seeds at this moisture content germinated without radicles and plumules penetrating the seed coat and gave vernalization response when exposed to high temperature, 35° C., for 10 and 20 days (S. M. Sircar and B. N. Ghosh, Nature 159: 605, 1947).

Further work by S. M. Sircar and S. K. Mukherjee (in press) on nitrogen metabolism of a winter rice variety, *Rupsail*, has shown that the total-N, protein-N, soluble non-protein-N, amide-N, amino-N and ammonical-N were higher in both leaves and stems of 8-hour day plants than in the controls. These nitrogenous substances increased in the leaves up to three weeks of photoperiod while an abrupt fall in total-N and protein-N was noted at the end of the fourth week. On the other hand, in the stems total-N and protein-N decreased and soluble non protein-N, amide-N, amino-N, and ammonia-N increased after successive weeks of photoperiod. These results in conformity with the work of S. M. Sircar and B. N. De (1947) indicate that greater depletion of total nitrogen in the leaves after the plants had considerably gained in dry matter in the first three weeks with a corresponding increase in all soluble nitrogen fractions in the stem is due to translocation of nitrogenous substances to growing points inducing a considerable earliness in this variety where flowering takes place within 6 weeks of 8 hours photoperiod.

SOME PRELIMINARY OBSERVATIONS OF PHENOLOGICAL DATA AS A TOOL IN THE STUDY OF PHOTOPERIODIC AND THERMAL REQUIREMENTS OF VARIOUS PLANT MATERIAL

by

M. Y. NUTTONSON

Formerly Senior Agronomist, Technical Collaboration Branch, Office of Foreign Agricultural Relations, U. S. Department of Agriculture

The effect of the relative length of day and night upon growth and reproduction in plants has been studied since 1920 when GARNER and ALLARD first focused the attention of plant physiologists on the phenomena of photoperiodism.

Our present day concepts in regard to the fundamentals of plant growth and plant responses to light duration are largely due to investigations conducted under controlled or semicontrolled conditions in the laboratory, greenhouse, or field.

The present objective of the writer is merely to suggest on the basis of preliminary studies of fairly extensive agronomic and horticultural data that there appears to be an "uncontrolled" field method which can be used to ascertain and to establish the nature of photoperiodic responses of various plants. These responses, it is believed, could be studied through the use of phenology and phenological records of horticultural and agronomic varieties of plants grown under uncontrolled field conditions in a great number of geographical-climatic areas.

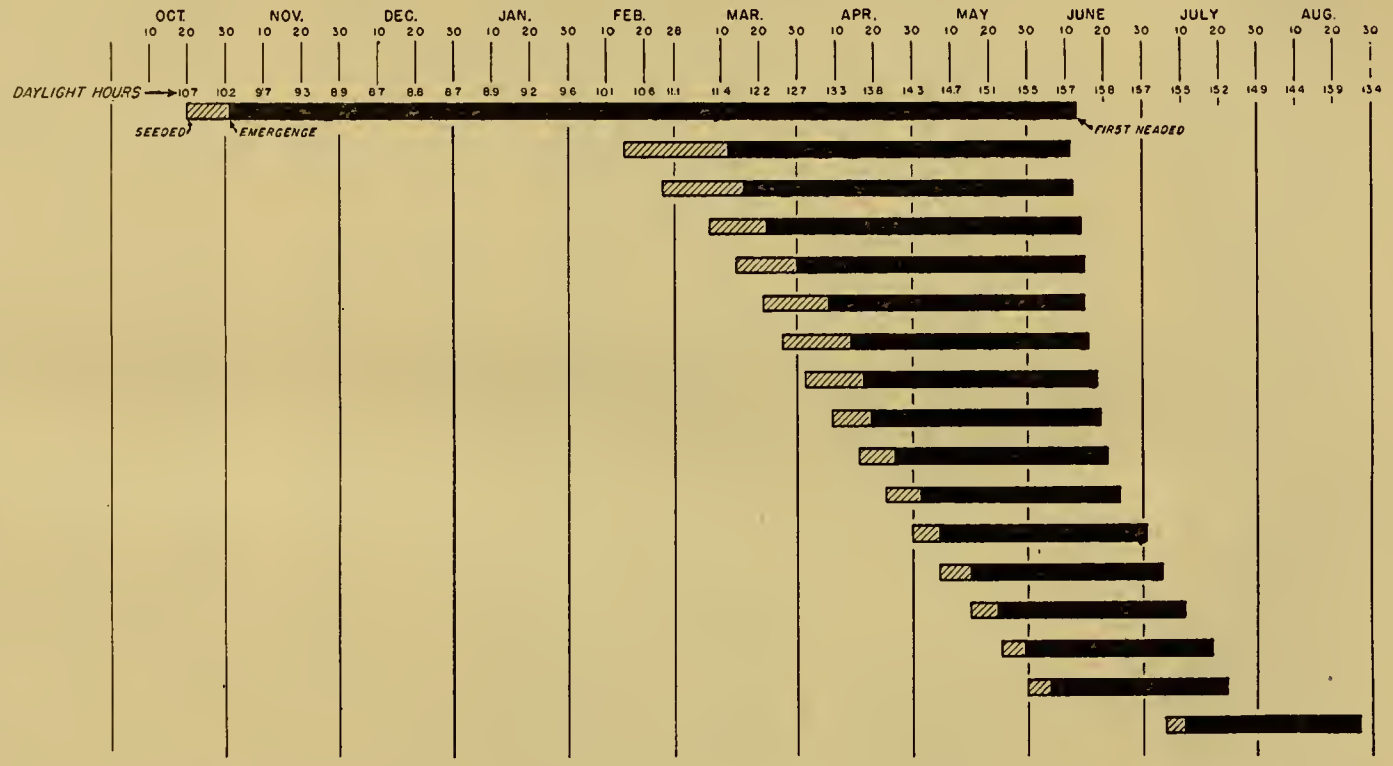
The dictionary defines phenology as a science dealing with the relation between climate and periodic biological phenomena. Dates of sowing or planting of crops, dates of germination or emergence, dates of stooling or tillering, dates of leaf bud opening, dates of shooting, dates of blossoming or heading, dates of terminal bud formation, dates of various distinct stages of biological or market maturity of genetically homogeneous clones or pure line horticultural varieties are the kind of phenological data the writer has in mind.

Phenological records are most often gathered as incidental data in the course of various agronomic and horticultural field studies. The utilization, if any, of such records has been so far mainly of a very limited and local nature. Studies of varietal adaptation, quantitative and qualitative yield studies, plant breeding studies, disease and pest problem studies, etc. are all sources of phenological material. Experimental and commercial plantings of the same varieties in various localities, plantings of the same varieties during various years in the same locality, and plantings of the same varieties during various seasons of the same year in the same locality as well as time of planting studies of the same varieties during any given

CHART No. I

PHENOLOGY OF MARQUIS WHEAT AT MARO[Δ], OREGON*

(TIME OF SEEDING STUDIES DURING 1926–27 SEASON)



* BASED ON DATA FROM ARTICLE BY B.B BAYLES AND J F MARTIN, JOURNAL AGRI RESEARCH, VOL 42, NO 8, APRIL 15, 1931, PP 483–500.

Δ LAT 45°30' ELEV. 1858 FT

year in any one locality—all provide sources of valuable phenological records.

Phenological data when properly organized and analyzed in the light of various latitudinal and climatic factors seem to suggest that mathematically determinable single or several interrelated ecological factors exert a definite influence on the growth behavior pattern of a given variety. Phenological data from a considerable number of various geographic locations are needed in order to be able to analyze and to ascertain the broader implications of these data in regard to certain fundamentals of growth, behavior, and environmental responses of a given variety. The preliminary nature of these phenological studies permits the writer to speak only in terms of some observations of trends of plant behavior rather than in terms of clear-cut conclusions as to the phenological pattern of behavior of various distinct varietal plant material. A demonstration of some of these various trends of phenological behavior of a few selected varieties of plants is all that is attempted at present.

TABLE 1

*Phenology of Marquis Wheat at Moro, Oregon**
(Time of Seeding Studies During 1926-27 Season)

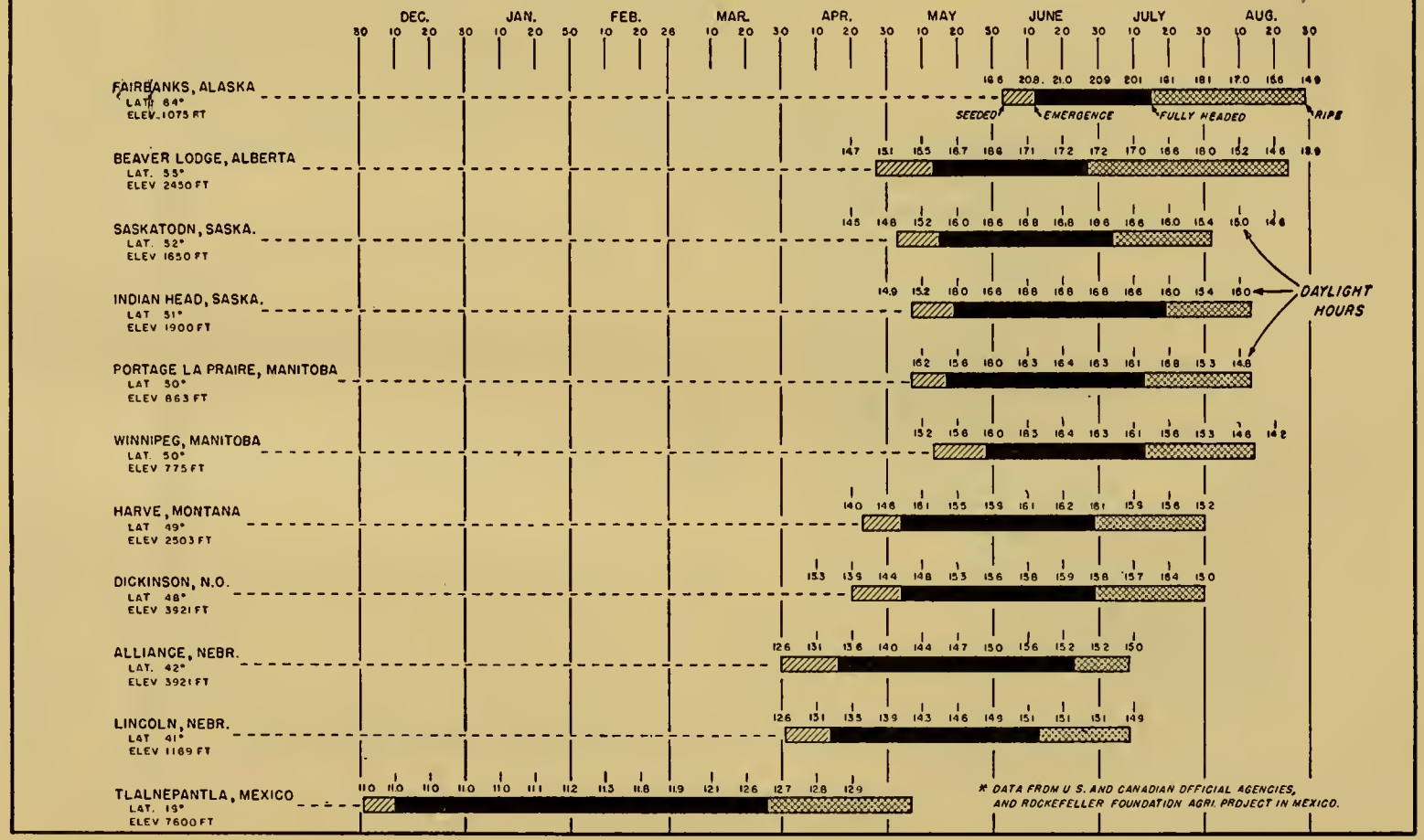
Moro, Oregon Latitude 45° 30′			*From Emergence to First Heading*			
DATE OF SEEDING	DATE OF EMERGENCE	DATE OF OF FIRST HEADING	DAYS	DAY-DEGREES	AV. LENGTH OF DAY (in hrs.)	AV. LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Oct. 20	Nov. 1	June 13	225	2070°	11.4	23,598
Feb. 15	Mar. 12	June 11	91	1598°	13.9	22,087
Feb. 25	Mar. 16	June 12	88	1581°	14.1	22,292
Mar. 7	Mar. 22	June 14	84	1571°	14.1	22,151
Mar. 14	Mar. 31	June 15	76	1495°	14.5	21,667
Mar. 21	Apr. 8	June 15	68	1380°	14.8	20,424
Mar. 26	Apr. 14	June 16	63	1323°	14.8	19,580
Apr. 2	Apr. 17	June 18	62	1339°	15.0	20,085
Apr. 9	Apr. 19	June 19	61	1340°	15.0	20,100
Apr. 16	Apr. 25	June 21	57	1313°	15.0	19,695
Apr. 23	May 2	June 24	53	1291°	15.2	19,623
Apr. 30	May 7	July 1	54	1390°	15.2	21,128
May 7	May 15	July 5	51	1399°	15.4	21,545
May 15	May 22	July 11	49	1462°	15.5	22,661
May 23	May 29	July 18	50	1602°	15.6	24,991
May 31	June 6	July 22	46	1530°	15.6	23,868
July 6	July 11	Aug. 27	47	1605°	14.5	23,725

* Phenological data upon which this chart and table are based were obtained from B. B. BAYLES and J. F. MARTIN, "Growth Habit and Yield in Wheat As Influenced by Time of Seeding" Journal Agricultural Research, Vol. 42, No. 8, April 15, 1931, pp. 483-500. — Day-degrees were calculated above 32°F.

As may be seen from Table 1 and Chart 1 the interval between the dates of emergence and first heading of Marquis wheat provides the least variable mathematical expression when measured in terms of a multiple of the

CHART No. 2

PHENOLOGY OF MARQUIS WHEAT IN A NUMBER OF NORTH AMERICAN AREAS *



average length of day and the summation of total day-degrees.[1] Measurements between these two phenological stages in terms of days or in terms of day-degrees alone provide mathematical expressions of considerable variability. Thus, the date of first heading of Marquis wheat appears to be associated with a response to more than one environmental factor, namely, to a combination of the average length of day and the summation of day-degrees. It appears, therefore, that the temperature must be taken into account in studies dealing with the relation of Marquis wheat to length of day. As may be observed in the table, the first heading on June 13 can be interpreted as having been brought about by a combination of 2070 day-degrees and 11.4 hours of average daylight while that of the first heading on August 27 as having been brought about by a combination of 1605 day-degrees and 14.5 hours of average daylight. Thus, one could say that the first heading of Marquis wheat is brought about by a combination of either relatively higher summation of day-degrees and shorter days or by relatively lower summation of day-degrees and longer days. In other words, the change from vegetative to reproductive stage may occur in Marquis wheat under a number of certain combinations of temperature and length of day conditions.

As may be seen from Table 2 and Chart 2, the interval between the dates of emergence and heading as well as the intervals between the dates of emergence and ripening provide the least variable mathematical expression when measured in terms of a multiple of the average length of day and the summation of total day-degrees.

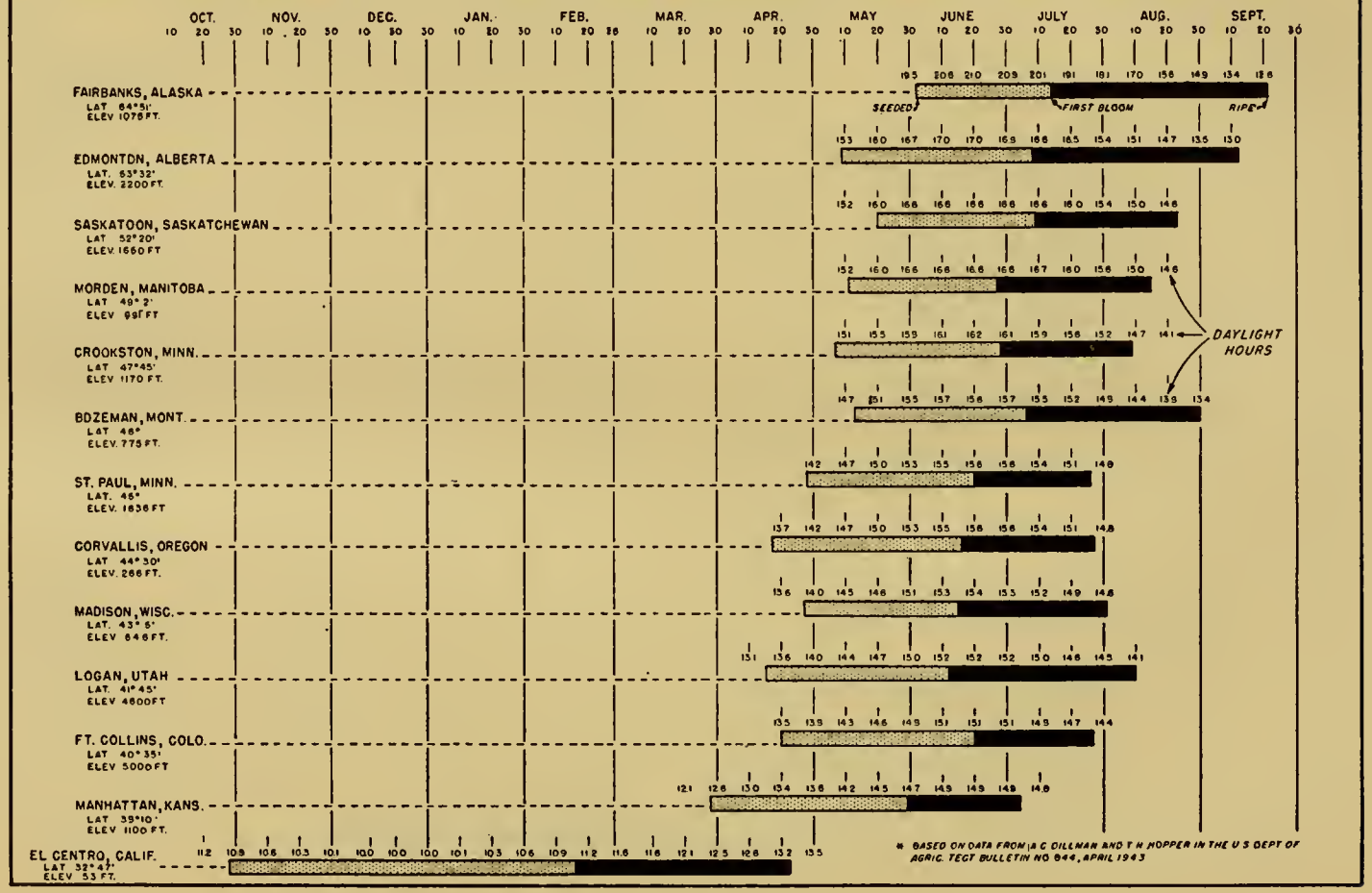
As already noted in the data of Table 1 it appears from the data of Table 2 that the heading as well as the ripening of Marquis wheat is brought about under a number of combinations of temperature summations and length of day conditions. Also, that the response of Marquis wheat to length of day seems to be influenced by the total day-degrees summation between the two phenological stages involved and therefore, the temperature must be taken into account in studies dealing with the relation of certain varieties of wheat to light duration. The day-degrees requirement of Marquis wheat from emergence to ripening seems to increase in a southward direction, that is, with the shortening of the length of day duration. It could, therefore, be suggested also that the response of Marquis wheat to temperature conditions seems to be influenced by the length of day.

As may be seen from Table 3 and Chart 3, the interval between the dates of seeding and first bloom of the flax varieties provides a least variable mathematical expression when measured in terms of a multiple of the average length of day and the summation of the total day-degrees. This seems to be also true in the case of the interval between the dates of seeding and ripening. It appears, therefore, with these four varieties of flax that the temperature must be taken into account in studies dealing with the relation of certain varieties of flax to light duration as the response of some flax

[1] The summation of day-degrees, also known as the remainder indices, consists of the summation of all mean daily temperatures above a certain "zero" temperature. In this paper 32°F. for wheat and flax and 40°F. for peas and eggplants have been used as "zero" temperatures. The procedure is to have the zero temperature subtracted from the mean daily temperature between certain phenological events and the remainder multiplied by the total number of days between dates of any two phenological stages under consideration.

CHART No. 5

PHENOLOGY OF FOUR VARIETIES OF FLAX (LINOTA, REDWING, BISON AND RIO) IN A NUMBER OF NORTH AMERICAN AREAS *



* BASED ON DATA FROM I. C. DILLMAN AND T. H. HOPPER IN THE U. S. DEPT OF AGRIC. TECT BULLETIN NO 844, APRIL 1943

TABLE 2

*Phenology of Marquis Wheat in a Number of North American Areas**

	DATE OF SEEDING	DATE OF EMERGENCE	DATE OF FULL HEADING	DATE RIPE	From Emergence to Full Heading: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES	From Emergence to Ripe: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Fairbanks, Alaska . Lat. 64°	June 3	June 12	July 15	Aug. 29	33	955°	20.3	19,386	78	2054°	19.0	39,026
Beaver Lodge, Alb. Lat. 55°	Apr. 27	May 13	June 27	Aug. 24	44	1176°	16.8	19,757	102	2296°	16.7	38,343
Saskatoon, Sask.... Lat. 52°	May 3	May 15	July 4	Aug. 2	50	1192°	16.6	19,787	89	2375°	16.4	38,950
Indian Head, Sask. Lat. 51°	May 7	May 19	July 19	Aug. 13	61	1434°	16.5	22,011	86	2394°	16.4	39,262
Portage la Prairie, Manitoba, Lat. 50°	May 7	May 17	July 13	Aug. 13	47	1405°	16.1	22,620	78	2398°	16.0	38,368
Winnipeg, Manitoba Lat. 50°	May 13	May 28	July 13	Aug. 14	46	1402°	16.2	23,712	77	2448°	16.0	39,168
Havre, Montana .. Lat. 49°	Apr. 23	May 4	June 29	July 31	52	1289°	15.8	23,386	85	2454°	15.7	38,528
Dickinson, N. D... Lat. 48°	Apr. 20	May 4	June 29	July 31	56	1395°	15.5	21,622	89	2540°	15.4	39,116
Alliance, Nebraska. Lat. 42°	Mar. 31	Apr. 16	June 23	July 9	68	1682°	14.6	24,657	97	2793°	14.7	41,057
Lincoln, Nebraska . Lat. 41°	Apr. 1	Apr. 14	June 13	July 9	60	1743°	14.2	24,751	86	2816°	14.5	40,832
Tlalnepantla, Mex.. Lat. 19°	Dec. 1	Dec. 10	Mar. 26	May 7	106	2121°	11.6	24,604	148	3711°	11.7	43,419

* The Canadian and United States phenological data upon which this chart and table are based were received in answer to specific requests made to Canadian and United States official agencies; likewise, the Mexican data were received from the Rockefeller Foundation Agricultural Project in Mexico. — Day-degrees were calculated above 32°F.

CHART No 4

PHENOLOGY OF ALASKA PEAS AT COLLEGE PARK, MARYLAND, 1925 *

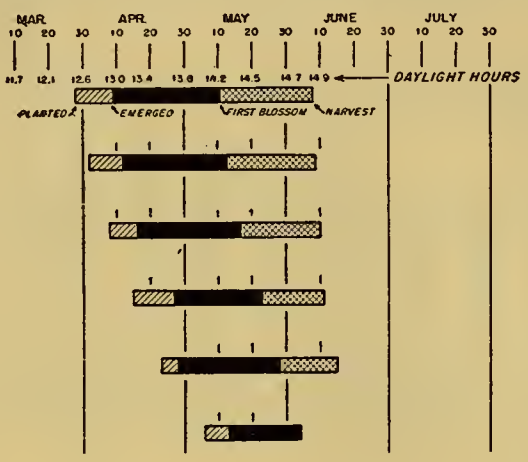
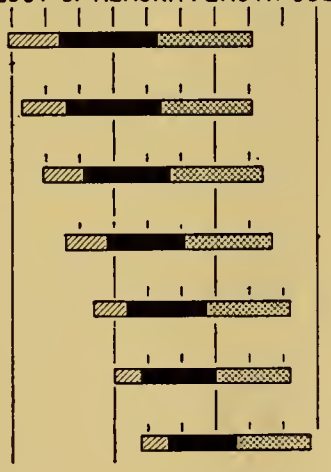


CHART No. 5

PHENOLOGY OF ALASKA PEAS AT COLLEGE PARK, MARYLAND, 1926 *



* BASED ON DATA FROM AN ARTICLE BY V R BOSWELL, -UNIVERSITY OF MARYLAND AGRIC EXPERIMENTAL STATION, BULLETIN NO 306, MARCH 1929

CHART No. 6

PHENOLOGY OF ALASKA PEAS IN A NUMBER OF NORTH AMERICAN AREAS Δ

Δ BASED ON DATA FROM PENN STATE COLLEGE, UNIVERSITIES OF ALASKA AND MARYLAND AND THE J. HARRIS SEED CO. OF ROCHESTER, N.Y.

TABLE 3

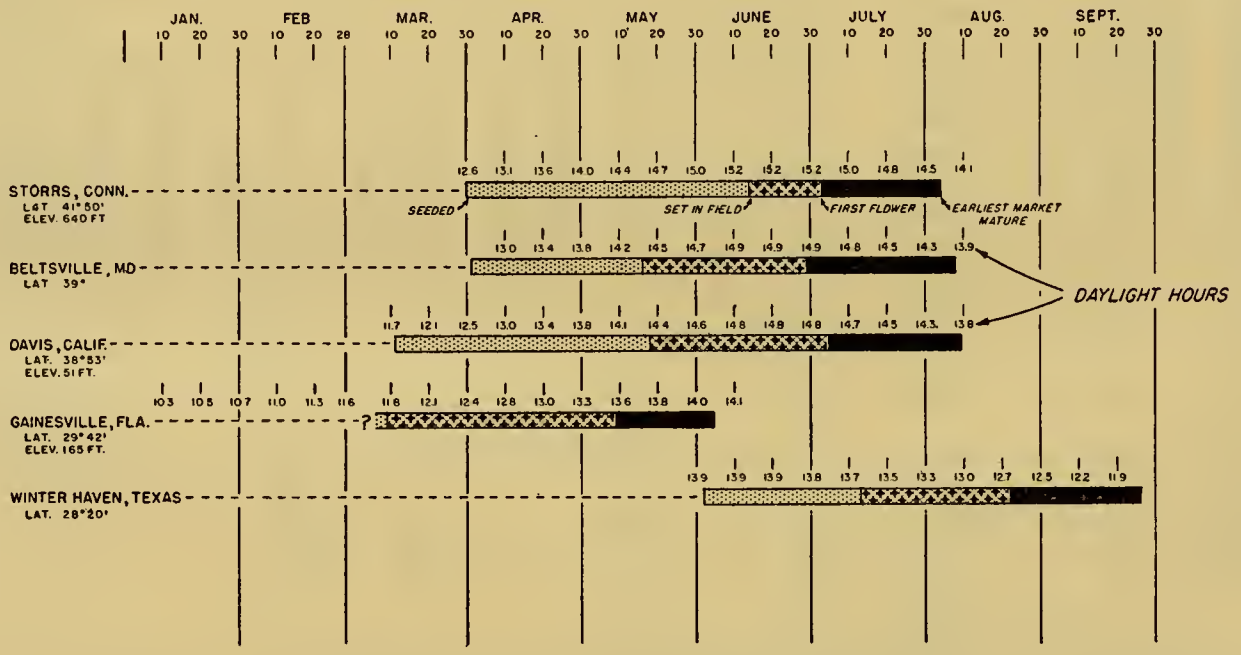
*Phenology of Four Varieties of Flax (Linota, Redwing, Bison, Rio) in a Number of North American Areas**

				From Seeding to First Bloom				From Seeding to Ripe			
	DATE OF SEEDING	DATE FIRST BLOOM	DATE RIPE	DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES	DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Fairbanks, Alaska ..... Lat. 64° 51′	June 2	July 14	Sept. 20	42	1171°	20.5	24,005	110	3175°	17.7	56,197
Edmonton, Alberta ..... Lat. 53° 32′	May 9	July 8	Sept. 12	60	1400°	16.5	23,100	126	3120°	15.7	48,984
Saskatoon, Saskatchewan .... Lat. 52° 20′	May 20	July 9	Aug. 23	52	1293°	16.6	21,464	97	3019°	16.1	48,606
Morden, Manitoba ..... Lat. 49° 2′	May 11	June 27	Aug. 15	47	1270°	16.4	20,828	96	2894°	16.0	46,304
Crookston, Minnesota ..... Lat. 47° 45′	May 8	June 28	Aug. 9	51	1408°	15.8	22,246	94	2955°	15.6	46,098
Bozeman, Montana ..... Lat. 46°	May 13	July 6	Aug. 30	54	1459°	15.0	21,885	109	3000°	15.1	48,300
St. Paul, Minnesota ..... Lat. 45°	Apr. 28	June 20	July 26	53	1522°	15.0	22,830	89	3109°	15.1	46,946
Corvallis, Oregon ..... Lat. 44° 30′	Apr. 17	June 16	July 27	60	1617°	14.7	23,770	101	3125°	14.8	46,250
Madison, Wisconsin ..... Lat. 43° 5′	Apr. 27	June 15	Aug. 1	49	1559°	14.5	22,605	96	3169°	14.8	46,901
Logan, Utah ..... Lat. 41° 45′	Apr. 15	June 12	Aug. 10	58	1327°	14.3	18,976	117	3537°	14.5	51,286
Fort Collins, Colorado ..... Lat. 40° 35′	Apr. 20	June 20	July 27	61	1329°	14.5	19,270	98	2888°	14.6	42,165
Manhattan, Kansas ..... Lat. 39° 10′	Mar. 28	May 29	July 5	67	1680°	13.5	22,680	100	3186°	14.0	44,604
El Centro, California ..... Lat. 32° 47′	Oct. 28	Feb. 16	Apr. 23	111	2112°	10.4	21,965	177	4876°	11.5	56,074

* Phenological data upon which this chart and table are based were obtained from A. C. DILLMAN and T. H. HOPPER "Effect of Climate on the Yield and Oil Content of Flaxseed and on the Iodine Number of Linseed Oil." U. S. Department of Agriculture Technical Bulletin No. 844, April 1943. — Day-degrees calculated above 32°F.

CHART No. 7

PHENOLOGY OF BLACK BEAUTY EGGPLANTS IN A NUMBER OF NORTH AMERICAN AREAS*



* BASED ON DATA FROM REPORTS OF THE BUREAU OF PLANT INDUSTRY, U.S. DEPT. OF AGRI., BELTSVILLE, MD.

TABLE 4
*Phenology of Alaska Peas at College Park, Maryland**
(Time of Seeding Studies During 1925)

DATE PLANTED	DATE EMERGED	DATE FIRST BLOSSOM	DATE OF HARVEST	From Emergence to First Blossom: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES	From Emergence to Harvest: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Mar. 28	Apr. 9	May 11	June 8	32	603°	13.6	8,200	60	1394°	13.8	19,237
Apr. 2	Apr. 12	May 13	June 9	31	594°	13.6	8,078	58	1376°	14.0	19,333
Apr. 8	Apr. 16	May 17	June 10	31	586°	13.8	8,087	55	1322°	14.1	18,640
Apr. 15	Apr. 27	May 23	June 11	30	535°	14.1	7,543	49	1254°	14.2	17,870
Apr. 23	Apr. 28	May 28	June 15	30	573°	14.2	8,137	48	1229°	14.3	17,575
May 6	May 13	June 4	.....	22	531°	14.6	7,753	..	....	...	.....

TABLE 5
*Phenology of Alaska Peas at College Park, Maryland**
(Time of Seeding Studies During 1926)

DATE PLANTED	DATE EMERGED	DATE FIRST BLOSSOM	DATE OF HARVEST	From Emergence to First Blossom: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES	From Emergence to Harvest: DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Mar. 29	Apr. 14	May 13	June 11	29	572°	13.8	7,894	58	1279°	14.0	17,906
Apr. 3	Apr. 16	May 14	June 11	28	571°	13.8	7,880	56	1261°	14.0	17,717
Apr. 9	Apr. 21	May 17	June 14	26	560°	13.9	7,784	54	1331°	14.1	18,836
Apr. 16	Apr. 28	May 21	June 17	24	559°	14.0	7,826	51	1263°	14.3	18,061
Apr. 24	May 4	May 27	June 22	23	550°	14.3	7,865	51	1267°	14.4	18,245
Apr. 30	May 8	May 30	June 22	22	530°	14.4	7,632	45	1180°	14.5	17,110
May 8	May 16	June 6	June 28	21	510°	14.6	7,446	43	1161°	14.6	17,009

* Phenological data upon which these charts and tables are based were obtained from VICTOR R. BOSWELL'S "Factors Influencing Yield and Quality of Peas"—Biophysical and Biochemical Studies, University of Maryland Agricultural Experiment Station, Bulletin No. 306, March 1929. — Day-degrees were calculated above 40°F.

varieties seems to be to the joint effect of light duration and temperature rather than to one of the two factors.

From the data of Table 3 it appears that the first bloom in Saskatoon, Saskatchewan, for instance, could be interpreted as having been brought about by a combination of 1293 day-degrees and 16.6 hours of average daylight while that in El Centro, California, as having been brought about by a combination of 2112 day-degrees and 10.4 hours. The multiples of the average length of day and the day-degree summation in the two instances are very much alike in their numerical expressions. Similarly, as may be seen from the table, the multiples of light duration and summation of day-degrees between the dates of seeding to ripening in Fairbanks, Alaska and El Centro, California, are of very similar magnitudes. However, while a combination of 3175 day-degrees and 17.7 hours of average daylight was required to bring about ripening in Alaska, the ripening in California required a combination of 4876 day-degrees and 11.5 hours of average daylight. One could thus suggest that in the case of these four varieties of flax the first bloom, as well as the ripe stage, is brought about by a combination of either relatively higher summation of day-degrees and shorter days or by relatively lower summation of day-degrees and longer days. In other words, the change from vegetative to reproductive stage seems to occur in some flax varieties under a number of certain combinations of temperature and length of day conditions.

TABLE 6

*Phenology of Alaska Peas in a Number of North American Areas**

			From Planting to Harvest			
	DATE PLANTED	DATE OF HARVEST	DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY (in hrs.)	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
Matanuska, Alaska . Lat. 61° 30′	May 18	July 20	63	912°	19.1	17,427
Rochester, N. Y. .. Lat. 43° 12′	Apr. 20	June 20	61	1145°	14.5	16,602
State College, Pa. .. Lat. 40° 45′	Apr. 19	June 21	63	1293°	14.3	18,490
College Park, Md. . Lat. 39°	Mar. 23	June 8	75	1359°	13.6	18,482

* Phenological data upon which this chart and table are based were obtained from reports of the University of Alaska, Pennsylvania State College, University of Maryland, and The Joseph Harris Seed Co. of Rochester, N. Y. — Day-degrees were calculated above 40°F.

The data of Tables and Charts 4 and 5 taken together as a unit for comparison purposes suggest that the interval between the dates of emergence and first blossom of Alaska peas provide the least variable mathematical expression when measured in terms of a multiple of the average length of day and summation of total day-degrees. The same seems to be true with the interval between the dates of emergence and harvest. It could be therefore suggested that the response of Alaska peas to the length of day is in-

TABLE 7

*Phenology of Black Beauty Eggplants in a Number of North American Areas**

				Set in Field to Earliest Market Maturity		*From Seeding to Earliest Market Maturity*			
	DATE OF SEEDING	SET IN FIELD	EARLIEST MKT. MATURE	DAYS	DAY-DEGREES	DAYS	DAY-DEGREES	AVERAGE LENGTH OF DAY	AVERAGE LENGTH OF DAY MULTIPLIED BY DAY-DEGREES
								(in hrs.)	
Storrs, Connecticut ..... Lat. 41° 45′	Mar. 30	June 14	Aug. 8	64	1798°	135	4123°	15.0	61,845
Beltsville, Md. ..... Lat. 39°	Apr. 1	May 16	Aug. 8	62	2102°	Temp. data prior to Set in Field unavailable.			
Davis, California ..... Lat. 38° 33′	Mar. 11	May 18	Aug. 9	85	2192°	152	4443°	14.2	63,535
Gainesville, Fla. ..... Lat. 29° 42′	.....	Mar. 9	June 4	86	2669°	Temp. data prior to Set in Field unavailable.			
Winter Haven, Texas ... Lat. 28° 20′	June 2	July 13	Sept. 26	74	2872°	117	4831°	13.0	62,803

* Phenological data upon which this chart and table are based were obtained from reports of the Bureau of Plant Industry, U. S. Department of Agriculture, Beltsville, Maryland. — Day-degrees were calculated above 40°F.

fluenced by the temperature conditions and hence the temperature must be taken into account in studies dealing with the relation of peas to light duration.

The data of Table 6 and Chart 6 also suggest the multiple of day-degrees summation and average length of daylight as the least variable expression for measuring the interval between two phenological stages in Alaska peas. As may be seen from the data in this table the interval between planting and harvest seems to have taken 912 day-degrees at an average length of day of 19.1 hours in Alaska and 1359 day-degrees at an average length of day of 13.6 hours in Maryland. Thus, again the response of Alaska peas to length of day appears to be associated with the temperature conditions to which they are subject. Hence, the temperature must be taken into account in studies dealing with the relation of certain varieties of peas to light duration. With these data too the day-degree requirement of Alaska peas from planting to harvest seems to increase in southward direction, that is, with the shortening of the length of day duration.

As may be observed in Table 7 and Chart 7 the interval between the dates of seeding to market maturity of the Black Beauty eggplant provides the least variable mathematical expression when measured in terms of a multiple of the average length of day and the summation of the total day-degrees. No comparison is attempted between dates of seeding and "set in field" as the latter does not represent a clear-cut end point of any phenological stage.

It appears that with the Black Beauty eggplant the amount of day-degrees required to bring about the earliest market maturity stage increases southward, that is, with the decrease in the duration of the average length of day. Hence, the temperature must be taken into account in studies dealing with the response of certain varieties of eggplants to light duration as it is the joint effect of the two factors that seems to be involved here rather than light duration or temperature alone.

Summary and Discussion

I. Through the assembling of phenological data already available for a number of varieties of various crop species some preliminary evidence is presented to show the possibility of using such data to disclose and to ascertain the photoperiodic and thermal requirements of an horticultural variety grown under uncontrolled field conditions.

II. Phenological data utilized in this paper pertains to the following plant varieties and geographical areas in North America: (*1*) Phenological data of Marquis wheat (*a*) from a time of planting study at Moro, Oregon; and (*b*) from experimental plantings at Fairbanks, Alaska; Beaver Lodge, Alberta; Saskatoon and Indian Head, Saskatchewan; Portage la Prairie and Winnipeg, Manitoba; Havre, Montana; Dickison, North Dakota; Alliance and Lincoln, Nebraska; and Tlalnepantla, Mexico. (*2*) Phenological data of four varieties (Linota, Redwing, Bison, and Rio) of flax from experimental plantings at Fairbanks, Alaska; Edmonton, Alberta; Saskatoon, Saskatchewan; Morden, Manitoba; Crookston and St. Paul, Minnesota; Bozeman, Montana; Corvallis, Oregon; Madison, Wisconsin; Logan, Utah; Fort Collins, Colorado; Manhattan, Kansas; and El Centro, California. (*3*) Phenological data of Alaska peas (*a*) from a time of planting study at College Park, Maryland; and (*b*) from experimental and commercial plantings at Matanuska, Alaska; Rochester, New York; State College, Pennsylvania; and College Park, Maryland. (*4*) Phenological data of Black Beauty eggplant from experimental plantings at Storrs, Connecticut; Beltsville, Maryland; Davis, California; Gainesville, Florida; and Winter Haven, Texas.

III. Measurements of the interval between vegetative and reproductive stages, as well as that between planting or emergence and ripening, suggest a multiple of the average length of day and the summation of day-degrees as the least variable numerical expression. The use of days or day-degrees alone as a unit of measurement provides mathematical expressions of greater variability than that of the multiple.

IV. Blossoming or heading in some varieties appear to be associated with a response to more than one environmental factor, namely, to a joint effect of the average length of day and the summation of day-degrees of the vegetative stage.

V. An analysis of the data used in this work suggests that the temperature must be taken into account in studies dealing with the relation of certain plants to light duration. It also suggests that the transition from vegetative to reproductive stage, as well as the transition from initiation of growth to biological or market maturity, may occur with some plant varieties under a number of combinations of temperature and length of day conditions.

VI. Summation of day-degrees required by all the horticultural varieties presented in this paper appears to increase in a southward direction, that is, with the decrease of the average length of day duration.

THERMOPERIODICITY

by

F. W. WENT

William G. Kerckhoff Laboratories of the Biological Sciences, California Institute of Technology, Pasadena, Calif.

In the previous discussions the effects both of temperature and of periodic light-changes on plant development have been described. In each case direct effects and delayed or after-effects were observed.

In discussing vernalization of seeds it was shown that during the first thermophase the future development of the plant is strongly influenced by temperature, and this effect may be enhanced or counteracted to some extent by the second photophase. To obtain optimal development a marked temperature change has to occur between early stages of germination and later growth. This temperature change is a long-term process, measured in terms of months.

In photoperiodism the daily change from light to dark is essential to bring about developmental processes, and the effects of photoperiod are influenced or even determined by temperature. Theoretically this is interpreted by assuming that during the light and the dark periods different processes take place, which have to be balanced to obtain specific responses. Whereas in photoperiodism stress is laid on the direct effects of light and darkness, in thermoperiodicity the daily light cycle is given, and the effects of temperature during the light and dark periods are considered. Since development can be completely changed by varying temperatures during the dark period, and since optimal growth in most plants only occurs when the temperature is lower during night, stress should be laid on this daily cycle of optimal temperatures, and this is done by referring to this cycle as thermoperiodicity. Before discussing this latter phenomenon in greater detail, other cyclic temperature effects have to be mentioned, beginning with those having approximately a yearly cycle.

For a good understanding of temperature effects on the development of plants the fundamental work of BLAAUW and co-workers at the Laboratory for Plant Physiology at the Agricultural College in Wageningen, Netherlands, is essential. This work has mainly been carried out with bulbs. The latter have the great advantage, that during the greater part of their development they do not need any light, since the initiation and early growth of shoots, leaves and flowers occurs inside the apparently dormant bulb, while they are being stored at any desired temperature. Therefore the investigation of the temperature requirements during this apparent dormancy does not necessitate air-conditioned greenhouses, which were not available until recently. For this reason BLAAUW's data are the most complete available at present on the optimal temperatures of the various stages in plant development.

Another reason for the importance of BLAAUW's work are his microscopic observations of the meristem during and immediately after each temperature treatment, so that he could distinguish between the direct and indirect temperature effects, and so that he could identify each optimal temperature with a definite morphological stage.

After more than 10 years of work along these lines BLAAUW (1931) concludes: "It is hoped that the time has passed, when the development of buds and defoliation are described without any knowledge of what goes on inside the bud, and the development of the leaf primordia, of which only their macroscopical appearance is being observed." "Before talking about periodicity and dormancy, in connection with the later behavior of sprouting leaves or flowers, it is imperative that first the life history of these organs inside the bud is studied. For this precedes sprouting."

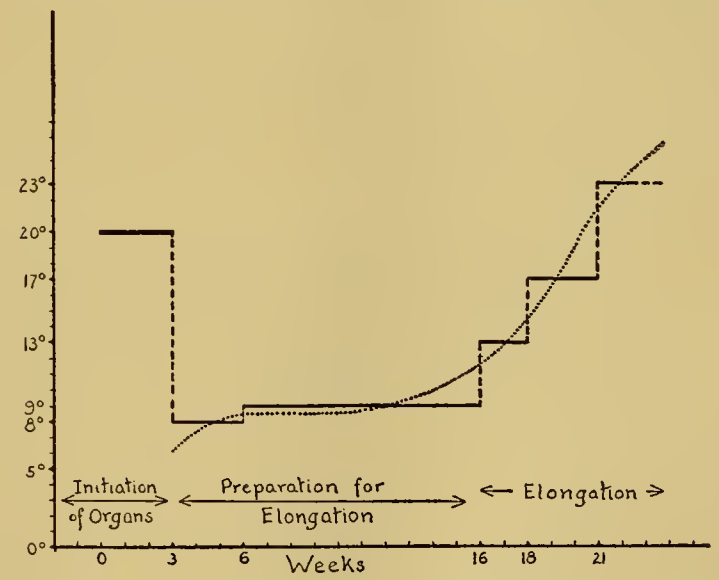


FIG. 1. — Optimal temperatures (ordinate, in degree centigrade) of the development of tulip bulbs (var. W. Copland) from the time of lifting from the ground to flowering (abscissa: time in weeks). Step-curve: experimentally determined optimal temperatures. Stippled curve: most likely actual optimal temperatures (*from* HARTSEMA, LUYTEN and BLAAUW 1930, p. 33).

In the experiments dry bulbs were placed in baskets and stored in temperature controlled rooms and incubators. All treatments were started immediately after the bulbs were lifted from the ground around July 1, when the current year's leaves had withered, and when the bulb seemed to have entered dormancy.

As a first example the development of the tulip bulb will be discussed. Figure 1 is taken from the publication of HARTSEMA, LUYTEN and BLAAUW (1930). Immediately after lifting, at the beginning of the experiment, next season's growing point has differentiated 3-4 leaf primordia, and is almost ready to initiate the flower. At that time the optimal temperature is highest, 20°C. When all flower part primordia have been initiated (about 3 weeks) the optimal temperature drops abruptly to 8°C., where it remains

for 3 weeks, after which it stays around 9°C. During those weeks the flower parts develop into a complete flower, and the stem elongates slightly. When the direct effect of temperature is measured by actual stem elongation, the optimal temperature is higher, but such higher temperatures retard subsequent elongation, compared with the 9° temperature. Therefore BLAAUW speaks here of an indirect or inhibited optimum. It compares with the low vernalization temperatures, which inhibit germination, but accelerate later growth. By the time the leaves become visible from between the scales, the optimal temperature shifts to 13°C., which is optimal for actual stem elongation, and the optimum shifts still further to 17°C., when the leaves have emerged 3 cm. from the bulb. When they are 6 cm. long the optimal temperature shifts again, to 23°C. This means that each developmental stage has its own optimal temperature; organ initiation needs the highest temperature, stem elongation and unfolding of the flower a lower one, and preparation for elongation, a stage which has no morphological signature, occurs best at the lowest temperature. It is likely that the steps between 9°, 13° and 17° are not abrupt, but gradual, so that the stippled curve of figure 1 probably approximates the actual conditions closer than the step-curve. The drop from 20° to 8° on the other hand is abrupt, and any intermediate temperature interposed between these two delays development.

For the hyacinth a slightly different curve was obtained, as seen in figure 2 (from LUYTEN, VERSLUYS and BLAAUW 1932). The whole curve lies about 4° higher than that of the tulip. But most important is the different behavior during the early weeks. As in the tulip, the highest optimal temperature occurs immediately after lifting, and in this case is 34°C. By the time the first flowers on the raceme have been initiated the optimal temperature shifts to 25.5°, and when the highest flower are visible as primordia on the raceme meristem, the optimal temperature drops to 17°. Three weeks later the lowest optimal temperature of 13°C., is reached. When the high temperature of 34° is maintained throughout the period of flower initiation, subsequent flower development is abortive, and racemes with flowers of poor quality are produced. Therefore the intermediate temperature of 25.5° is a compromise between the optimal temperatures of at least two different processes, which proceed simultaneously inside the bulb: flower initiation with a very high temperature optimum, and preparation for further flower development, with a much lower optimum.

Before discussing these results any further, another paper from the same laboratory, by VERSLUYS (1927) must be mentioned. She studied the optimal temperatures for root initiation and root elongation throughout the whole development of the hyacinth bulb. It was found that the optimal temperature for root growth remained approximately constant at 27° C. During the part of the life cycle of the bulb which was investigated, few new roots were initiated, but the greatest number formed occurred again at about 27°C.

Viewing these results together, it can be said that each physiological process in the hyacinth bulb has its own optimal temperature, which differs from that of other processes. Therefore the over-all optimal temperature of the whole bulb is a compromise between the optima of the individual proc-

esses, as was clearly expressed in the flower-stand formation. Since not all flowers are initiated at the same time, some are already so far advanced that they need low temperatures for further development, while other flowers still are in the process of initiation, and consequently require high temperatures. While the later stages of elongation proceed best at 13°C., the temperature should be 27°C. for best root growth. Since root development does not seem to be controlling bulb growth, and sufficient roots are formed at the optimal temperature for elongation, no compromise between root and stem elongation temperatures is necessary.

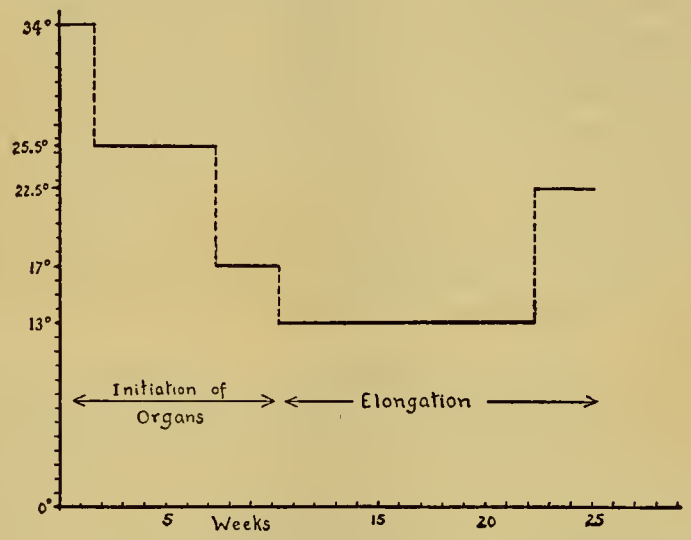


Fig. 2. — Optimal temperatures (ordinate, in degree centigrade) during the development of byacinth bulbs. Abscissa: time in weeks since lifting of bulbs from the ground (*from* Luyten, Versluys and Blaauw 1932, p. 51).

Whereas the curves shown in figures 1 and 2 show the shift in optimal temperatures, many diagrams showing the progress of individual processes at different temperatures are found in Blaauw's papers, and figure 3 (from Blaauw, Luyten and Hartsema 1930) shows a graphical presentation of the flower development as a function of temperature. It shows the range of temperatures in which flower development can proceed with an optimum about 12° wide. The curves of figure 4 (from Blaauw 1924) show the shift in optimum when observations are made in different intervals. From such curves it also would be possible to construct the curve of figure 2, but it would be less accurate.

For other bulbs the same type of an analysis was carried out. Daffodils (variety King Alfred) show a behavior similar to that of tulip and hyacinth, except that flower initiation already has taken place in the field, so that the optimal temperature starts as low as 13°C., lowering to 11° after eight weeks and shifting to 10° when leaves become visible. After 2 weeks the optimum increases to 17° and when leaves are 6 cm. to 20°C (*see* Blaauw, Hartsema and Huisman 1932). In stark contrast with the bulbs from temperate climates the tropical *Hippeastrum* (Blaauw 1931) has no obvious resting period but 2 to 3 times per year a whole cycle of leaf and flower formation is completed, at completely even temperatures.

PLATE 12 opposite page 149 perfectly illustrates the temperature effects in terms of bud development (magnification 14 ×). This is a reproduction of figures 4-14 from LUYTEN, JOUSTRA and BLAAUW (1926), and it shows the state of the growing point of a tulip bulb after a four week storage at constant temperatures ranging from 1.5° C. to 35° C. The figures show what can be observed at 14 times magnification after all bulb-scales and enclosing leaf bases have been removed around the growing point. The scars of the removed foliage leaves are indicated and marked LL1, LL2, etc. The main vegetative growing point producing the shoot for the next year is marked VP, the lateral growing point which would have developed 2 years later is VPA (with its bulb scales R_1 and R_2). After the 4th or 5th foliage leaf (LL4 or LL5) was initiated, the growing point widened and the petals (TI and TII), stamens (M_1 and M_2) and carpels (VD) were initiated.

At 1.5°, 31° and 35° C. no change in the growing point had taken place during the 29 days storage; the growing points were in stage I (vegetative). At 5° and 28° the 4th or 5th foliage leaf had developed, and the growing point was just advanced to where it changes to the flowering condition. At 9° the growing point was in stage III (only petals initiated), at 25.5° it had reached stage VI (all flower parts, except carpels, well developed), and between 13° and 23° they were all in the same advanced stage of development (stage VII).

Another interesting fact can be observed as concerns the effect of temperature on flower initiation. When the temperature is high, the normal trimerous flower is formed (23° and 25.5°), but at low initiation temperatures (9°-13°) the flowers are predominantly tetramerous. At intermediate temperatures (17°-20°) intermediate numbers of flower parts are found. This was reported in detail by BLAAUW, LUYTEN and HARTSEMA (1932), where they showed that some tulips (like "Pride of Haarlem") were almost completely tetramerous at 13° C. initiation temperature, at which temperature the "Will. Copland" and other varieties of tulips were trimerous. At high temperatures (28°) tulip varieties initiated consistently a smaller number of flower parts.

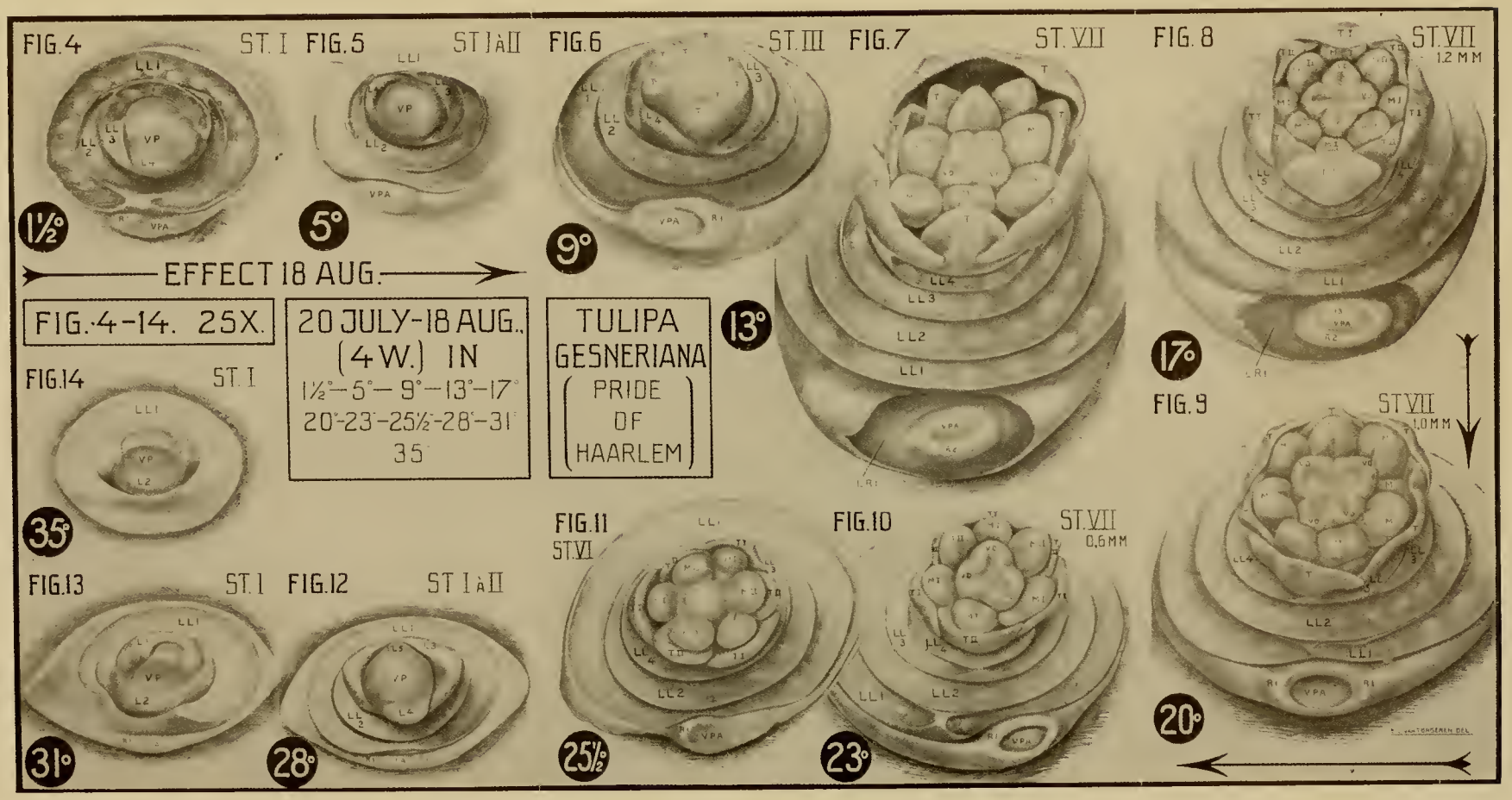


FIG. 4
ST. I
1½°
FIG. 5
ST. I & II
5°
FIG. 6
ST. III
9°
FIG. 7
ST. VII
13°
FIG. 8
ST. VII
1.2 MM
17°
EFFECT 18 AUG.
FIG. 4-14. 25X.
20 JULY-18 AUG., (4 W.) IN
1½°-5°-9°-13°-17°
20°-23°-25½°-28°-31°
35°
TULIPA GESNERIANA
(PRIDE OF HAARLEM)
FIG. 14
ST. I
35°
FIG. 9
ST. VII
1.0 MM
20°
FIG. 11
ST. VI
25½°
FIG. 10
ST. VII
0.6 MM
23°
FIG. 13
ST. I
31°
FIG. 12
ST. I & II
28°

The rhythmical development in tulip and hyacinth is controlled by variations in temperature, so that their strictly yearly cycle is synchronized with the progress of winter and summer in the temperate zones where they thrive. In *Hippeastrum,* an inhabitant of tropical regions with even temperatures throughout the year, an autonomous rhythm of the meristem causes a regular sequence of initiation of 3-4 leaves after which a flower stand is formed, after which, again, 3-4 leaves are produced, etc. This sequence can not be changed by temperature treatment.

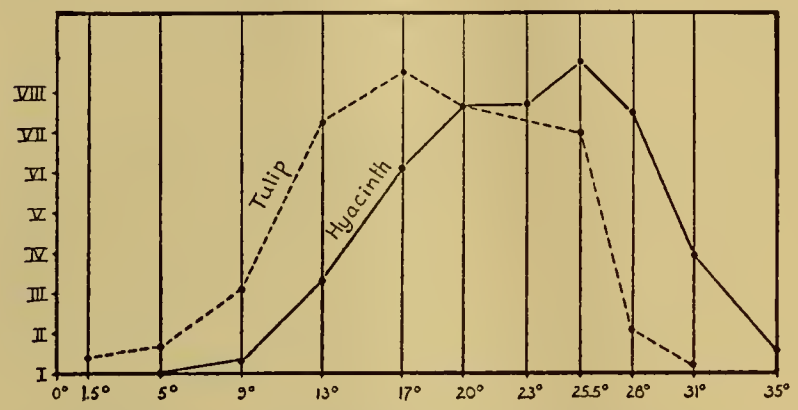


Fig. 3. — Actual development (ordinate: condition of growing point, stage I being vegetative, VIII being complete flower initiation) of the growing point in tulip and byacinth, as a function of storage temperature (abscissa, in degree centigrade). For the tulip the broken curve is recorded after 4 weeks, for the hyacinth the solid curve represents 8 weeks development at tbe different temperatures (*from* Blaauw, Luyten and Hartsema 1930, p. 51).

One of the most interesting results of Blaauw's work is, that from the curves of figure 3 it can be deduced that development can be arrested by both low and high temperatures. The cessation of development near freezing is not amazing, since it occurs in most plants. But all growth can be stopped by keeping bulbs at 35°C., which temperature is not injurious at all to the bulbs. As soon as the temperature is lowered to a proper one for the stage of development, growth is resumed as if no interruption has occurred. In a series of experiments bulbs were inhibited for 6 months by either high or low temperatures and then shipped to the Southern hemisphere. In this way their rhythm was shifted half a year, and the bulbs kept time with the shifted sequence of seasons, enabling successful shipping to the opposite hemisphere, which had not been possible before (Blaauw, Luyten and Hartsema 1930).

From a practical standpoint this spectacular success is not the most important. Of greater significance for the bulb industry is the fact that some of the most important stages in the development of a bulb are passed during its storage period. This had been realized by practical growers since Dames in 1909, but it was Blaauw who furnished the theoretical background and who rationalized the treatment. Adjustments to the treatment in storage are possible, which improve the later performance of the bulb in the field. If the bulbs have to be planted in a rather warm climate, part of the cold treatment they need (and usually receive in the field in colder climates) can

be administered during storage. In this way performance in practically any climate can be guaranteed. This is actually put into practice now so that shipments of bulbs can be treated individually to insure best flowering at the point of destination (*see e.g.* VAN SLOGTEREN 1935, 1936).

Many more important results were obtained by BLAAUW and co-workers on development and temperature, but the previous review summarizes the results most important for interpretation of thermoperiodicity.

Another set of phenomena, which are closely related to vernalization, are the chilling requirements for development of buds of deciduous trees. In most of these plants the buds are dormant for a considerable part of the winter, and can be forced into growth only after having been subjected to freezing temperatures. In some cases the low temperatures may have no other

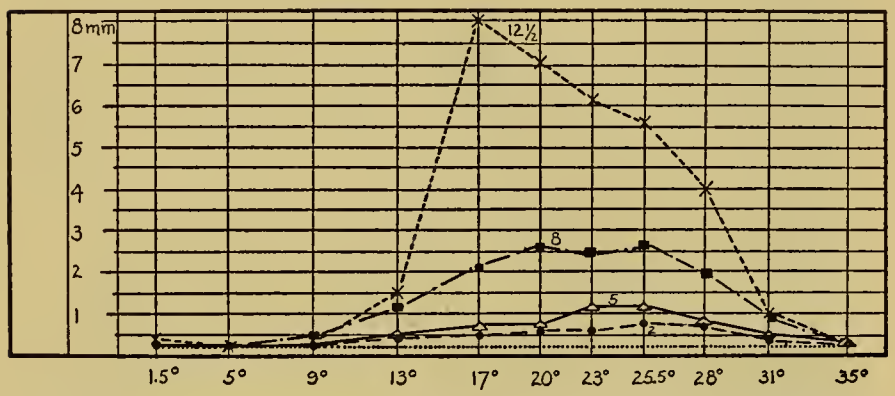


FIG. 4. — Length of the growing point and flower cluster (ordinate) in the hyacinth (var. Queen of the Blues), after they have been kept for various lengths of time at 11 different temperatures (abscissa, in degrees centigrade). Stippled line: original length; dots and broken line: after 3 weeks; triangles and solid line: after 5 weeks; squares and dash-dot line: after 8 weeks; crosses and broken line: after 12½ weeks (*from* BLAAUW 1924, p. 35).

effect than supplying a stimulus, so that a definite time after being subjected to a sudden drop in temperature, irrespective of the duration of this lower temperature, development occurs. The flower buds of the orchid *Dendrobium crumenatum* offer a clear-cut example (COSTER 1926, KUIJPER 1933). Nine days after a sufficiently rapid drop in temperature (usually associated with a heavy rainfall) the flowers of this orchid open, causing a sudden burst of flowering over a wide area. Some other orchids seem to behave in the same way, and probably other plants as well (gregarious flowering of *Coffea liberica*). In these cases the flower buds develop gradually up to a certain point, beyond which no growth is possible under the prevailing temperature conditions. The longer the temperature drop is delayed, the more flower buds will have reached the critical size, and the more abundant the flowering is after the temperature drop.

An intermediate case between the orchids and the deciduous trees is found in the lily of the valley, *Convallaria majalis* (HARTSEMA and LUYTEN, 1933). Their rootstocks become dormant in summer, when the current year's flowers and leaves have withered. Only after a one-week period of 0.5 to -2°C., or three weeks at 5° do the buds on these rootstocks start to grow. The optimal temperature for this effect seems to lie so close to freez-

ing that it is hard to see what physiological process could be responsible for the breaking of the dormancy. A similar phenomenon is known for *Gladiolus* corms (Denny 1942). When these are stored at warm soil temperatures, no development takes places. But short periods, of 24 hours or less, at 0-5°C., will break their dormancy. These cases may be comparable with the chilling requirements of some seeds, which will not germinate until they have been subjected to freezing (Crocker 1916). In this case hard-seededness has been held responsible for the dormancy, the freezing softening the seed coat.

Most deciduous trees of the temperate zone pass through a period of dormancy, during which time the buds cannot, or only with great difficulty, be made to develop. This is a secondary induced dormancy. In spring, soon after the buds have broken, axillary buds enlarge on the young shoots, and in early summer they have reached full size. By that time these buds are not dormant, but defoliation, or placing cut branches in water in the greenhouse, will cause almost immediate development into shoots. Two months later the buds, when subjected to the same treatment, will not develop even under favorable conditions. At the time of leaf fall the buds have reached the stage of deepest dormancy. In trees growing out of doors this dormancy decreases, until it has completely disappeared in spring. When branches or small trees are kept in the greenhouse, the dormancy does not disappear. In nature the dormancy may not be broken by the time of spring when the winter has been exceptionally warm. This gives rise to the phenomenon of "delayed foliation" (Chandler *et al.* 1937). Consequently many of these deciduous plants requiring a cold winter cannot be grown in climates with an equitable climate, such as subtropical regions and higher altitudes in the tropics.

Precise laboratory experiments on the chilling requirements of deciduous trees have not been carried out as yet. Numerous observations in nature have led to the following conclusions:

Only temperatures below 5-8°C., seem to be effective in breaking dormancy. These low temperatures must last for a sufficient number of hours, so that for each species and variety of plant a minimal number of hours below 5°C., can be assigned, which are required before the tree will leaf out. These hours have not necessarily to be consecutive, but the effect is cumulative. Varieties native to colder climates have a longer chilling requirement than those from climates with warmer winters. Therefore northern varieties grown in the south usually show delayed foliation (late and erratic breaking of buds in spring), whereas southern varieties may be killed farther north when their chilling requirements have been met before the danger of late frosts is past. Although the purely factual description of chilling requirements is very incomplete as yet, the physiology of the buds is better investigated. No reference will be made to the numerous papers describing the chemical composition of dormant tissues and of tissues whose dormancy has been broken, naturally or by artificial means. Nor will the many artificial methods employed to break dormancy be enumerated.

Bennett and Skoog (1938) found that buds kept dormant by leaving pear trees during winter in a heated greenhouse, could be made to sprout by application of yeast extract. Guthrie (1940) suggested that the glu-

tathione of yeast extract was the active agent breaking dormancy, but BENNETT, OSERKOWSKY and JACOBSON (1940) showed that the effect of yeast extract was due to a compound differing from glutathione.

Interpretation of these facts is hardly possible as yet. On the one hand it would appear that the dormancy induced in buds in the course of the summer is due to a growth inhibiting substance which accumulates in the fully developed buds. This substance is probably not identical with auxin, since auxin extractions at the time of deepest dormancy show the lowest auxin content. Yet it is possible to keep buds dormant beyond their normal seasonal loss of dormancy by spraying with auxin-like substances (GUTHRIE 1938). This auxin-induced dormancy therefore is different from normal dormancy.

The effectiveness of ethylene, ethylenechlorohydrin and similar substances in breaking bud dormancy could indicate destruction of inhibitors, as has been shown to be the case in the breaking of dormancy of potato tubers (MICHENER 1942). On the other hand the experiments of BENNETT and SKOOG (1938) and GUTHRIE (1940) indicate that application of materials which can be considered to contain growth promoting substances can break bud dormancy. From this one would be led to assume that dormancy is not due to accumulation of inhibitors, but to a lack of growth substances. It is conceivable that both mechanisms occur, but much work remains to be carried out before binding conclusions are possible.

Finally these findings will have to be correlated with the temperature effects. Not enough facts are at hand to even suggest a hypothesis how low temperatures could remove inhibitors or cause the production of growth promoting substances.

Already very early in the periodic development of plants with chilling requirements, periods of low temperature are necessary. In peach seedlings (LAMMERTS 1942) embryo-cultured seeds did grow immediately, but they soon became dormant. When these dormant seedlings were placed in cold storage at 5°C., 20-40 days sufficed to break their dormancy. The seeds of *Convallaria majalis* will start to germinate at medium temperature, but the epicotyl soon becomes dormant and will not continue development until exposed to low temperatures (BARTON and SCHROEDER 1942).

For a fairly complete discussion of all these facts we can go back to SACHS (1860). He was the first to study in detail (with a hardly adequate technique) the temperature relationships in the growth and development of plants. If we consider how primitive the methods were with which he had to obtain and maintain the various temperatures, his results and conclusions are truly remarkable. By using many different plants, he initiated a comparative growth physiology. The greater part of his work was carried out with seeds and seedlings, but in some further observations and considerations he extended his treatment of the temperature relationships of the growing plant until its maturity. SACHS realized, that each growth stage of the plant has its own temperature characteristics, which he considered to be adequately qualified by: minimal (z), optimal (y) and maximal (x) temperatures. As stages he considered seedling growth (S), vegetative growth (V), blossoming (B) and fruiting (F). He even distinguished a sub-stage: germination (G) which was somewhat different from seedling growth. Each plant could then be characterized as follows:

$$G\ \begin{matrix} x \\ y \\ z \end{matrix} \qquad S\ \begin{matrix} x_1 \\ y_1 \\ z_1 \end{matrix} \qquad V\ \begin{matrix} x_2 \\ y_2 \\ z_2 \end{matrix} \qquad B\ \begin{matrix} x_3 \\ y_3 \\ z_3 \end{matrix} \qquad F\ \begin{matrix} x_4 \\ y_4 \\ z_4 \end{matrix}$$

As example (expressed in degree centigrade) he gave:

Corn	G $\begin{matrix} 46 \\ 34 \\ 9.5 \end{matrix}$	S $\begin{matrix} 46 \\ 34 \\ 14.5 \end{matrix}$
Wheat	G $\begin{matrix} 42.5 \\ 29 \\ 5 \end{matrix}$	S $\begin{matrix} 42.5 \\ 29 \\ 10 \end{matrix}$

For certain early spring flowers, such as *Daphne, Galanthus* and *Hepatica* he concluded that $Z_2 > Z_3 < Z_4$.

The last few paragraphs of this paper of SACHS are worth quoting: "If we presume that all numerical values of the above scheme are known, it will be immediately possible to determine, whether a given climate offers the necessary growing conditions for a particular plant. In addition it would be necessary to add the specific time-relations, investigating for each x, y, and z how much time is required to complete phases G, S, V, B and F."

"Once all these data are known, we can hope that the law can be found, according to which temperature and development of a species are linked. The above scheme only serves to arrange the collected data in a logical manner. Using these known data it would be simple to discover the shortest possible time for development of the plant. This question cannot be answered without detailed analysis of the response of the plant, but offers much of interest in physiological respect."

The work of BLAAUW has answered some of the questions asked by SACHS, and has supplied the necessary data for V and B in a number of bulb species.

All previously mentioned facts show, that in the course of development of a plant there is a succession of processes, each of which may have a different temperature range. In some cases these ranges are so far apart, that under constant temperature conditions no continued development is possible, in other cases we find only a shift in optimal temperature from month to month. Such a shift in temperature characteristic can be expected whenever different processes succeed each other, no matter how short the duration of each process. Thus in photosynthesis the "Blackman" reaction has a Q_{10} of over 2, whereas the light reaction has a Q_{10} of about 1. In photoperiodism HAMNER and BONNER (1938) have shown that the dark reaction has a high temperature optimum, whereas the temperature during the photoperiod is of secondary importance in flower induction. This shows that the light and dark processes in flower induction can be separated by their temperature dependance. In general the photoperiodic response is greatly dependent upon temperature, and may be modified or even reversed by extreme temperatures (*see* pages 48-51).

Whereas in many plants the growth rate stays rather constant from day to night, in others the greater part of stem elongation occurs during night. Therefore, the temperature during night can be expected to have a marked influence on the growth rate of the plant as a whole. During day photosynthesis most likely does not have the same temperature optimum.

This consideration shows already that we can expect different optimal temperatures during day and night. This is the basis for thermoperiodicity.[1] Actually in most plants investigated thus far optimal growth and development occurs when day temperatures are considerably higher than night temperatures. For future discussion it seems advisable to refer to the light period, which usually, but not necessarily, coincides with the daytime, as the *photoperiod,* and to the temperature prevailing during this period as *phototemperature.* Since in thermoperiodicity the dark period is equally important as the photoperiod, and has to be referred to often, the term *nyctoperiod* is suggested. The temperature during the nyctoperiod is the *nyctotemperature.* This same term can be used in photoperiodism discussions.

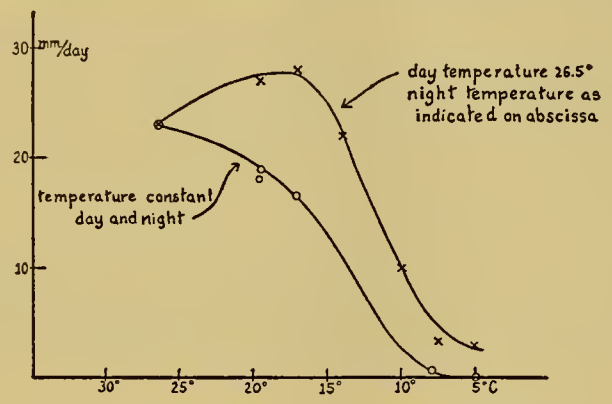


Fig. 5. — Relationship between stem growth rate (ordinate, in mm./day) and temperature (abscissa, in degree Centigrade) of tomato plants. The circles represent plants kept both day and night at the indicated temperature. The crosses show growth rates of plants kept during eight day hours at 26.5°C. and during night at the temperatures indicated on abscissa. Squares: plants kept during day at 19-20°, during night at 26.5°C. (*from* Went 1944, p. 140).

In work designed to find the optimal growing conditions for tomato plants (Went 1944) the optimal nyctotemperature was determined as 17-18°C., whereas the optimal phototemperature was closer to 26°C. than to 17° (*see* figure 5). These temperature relations were worked out in greater detail in later publications (Went 1944*a,* 1945*a*). The nyctotemperature optimum was high in the seedling stage (about 30°C.), and during the course of development gradually fell to 18° for the *San Jose Canner,* and to 13° for the *Illinois-19* tomato. This optimum was also influenced by the light intensity during the photoperiod, being lower for lower light intensities. The previous temperature treatment equally determined the response to the nyctotemperature. The conditions optimal for stem elongation were also optimal for fruit set and fruit growth.

An analysis of the temperature response of the chili pepper (*Capsicum annuum*) gave essentially the same results (Dorland and Went, 1947). Like the tomato, optimal growth was obtained at a phototemperature of

[1] On consideration of priority the term photoperiodism is now favored over photoperiodicity. On the same basis we should accept thermoperiodicity (Went 1944). Besides the word periodism does not occur in Webster so that periodicity is preferable on linguistic grounds.

26°, and the optimal nyctotemperature dropped from 30° in young plants to 8° for full grown plants; the same gradual decrease in optimal nyctotemperatures was found in blossoming, fruit set and fruit development.

In botanical literature practically no references are found to thermoperiodicity. SCHIMPER (1898) refers to observations of a peach grower, showing that optimal development of peach fruits requires a gradual rise in temperature from blossoming to fruit ripening, and a daily temperature drop from day to night, with an amplitude of about 3-5°C.

BONNER (1943) presented data, from which it can be concluded that *Cosmos* grows to about twice the weight at an 18° nyctotemperature and 26° phototemperature, when compared with constant 18° or 26°C. temperatures.

Not only growth but also other processes such as rubber formation in guayule (*Parthenium argentatum*) are strongly thermoperiodic (BONNER 1944). Rubber is formed at the fastest rate at nyctotemperatures between 5 and 10°C., and is very slight above 15°C. But rubber formation only occurs provided the phototemperatures are fairly high (18-26°C.).

Many plants do not grow or even die when the nyctotemperature is 26° or higher. LEWIS and WENT (1945) showed that *Baeria chrysostoma* and various other California spring annuals do not germinate, and young or older plants die when subjected to 26° nyctotemperatures. This is not due to diseases or pests, for Loo (1946) showed that even under sterile conditions *Baeria* plants die at such high nyctotemperatures. Since the lethal effect of high nyctotemperatures can be counteracted by lengthening the photoperiod, it seems possible that excessive respiration, coupled with deficient carbohydrate supply of the growing regions, is responsible for death.

ROBERTS (1943) in a short note reported on experiments with a wide variety of plants grown at either 24 or 13°C., at day or at night. He concluded that "The temperature during the dark period of the day is an important factor affecting bloom induction as well as some other reactions."

In commercial greenhouse culture it is well known that during day and night the temperatures should be kept at different levels. In LAURIE and KIPLINGER (1944) the following optimal temperatures in degree Centigrade are given:

	DAY	NIGHT
Violet	8.5–14	4.5–10
Snapdragon	14 –16	7 –9
Lathyrus	13 –15.5	9 –10
Roses	21 –23	14.5–16.5

ORCHIDS:—

Seedlings in general	21 –29
Seedlings of Odontoglossum	13.5–15.5
Mature plants of Cattleya	15.5–18.5
Mature plants of Odontoglossum	10

In many instances only optimal nyctotemperatures are given, apparently because they are considered more important, and since day temperatures are so hard to control. In some cases special mention is made of difference in optimal phototemperature according to light intensity (*Lathyrus* 13° on cloudy, 15.5° on sunny days); in another instance a differentiation of the

optimal nyctotemperature according to light is recorded (for *Phalaenopsis* 15.5°-18.5° during winter and 21° during summer).

Many more quotations could be made from the published experience of greenhouse growers, but in the botanical literature little more has appeared concerning thermoperiodicity.

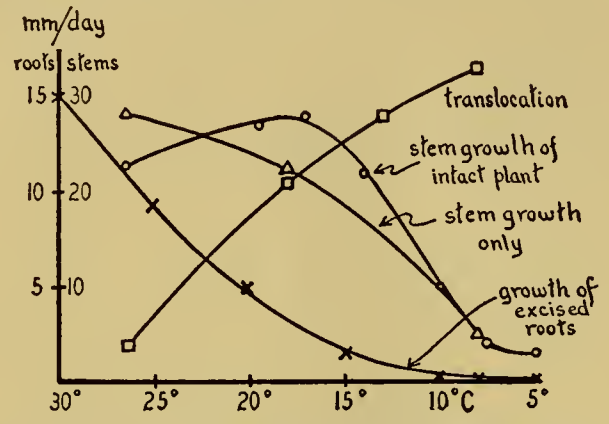


FIG. 6. — Relations between (night) temperature (abscissa in degree Centigrade) and (1) total growth of intact plants (circles), (2) direct effect on stem elongation (triangles), (3) growth of isolated roots (crosses), and (4) translocation (squares). (*from* WENT 1944*a*, p. 612).

The explanation of various phenomena observed in thermoperiodicity can be found in WENT (1944*a*, 1945*a*). During daytime photosynthesis seems to be the limiting factor for development. This is only true when the nyctotemperature is within the optimal range so that the assimilates can be utilized to best advantage. When the nyctotemperatures are too low, photosynthesis does not limit development any more (WENT 1945).

In darkness the fairly low optimum temperature in tomatoes is caused by the competition between two individual processes (*see* figure 6). Most of the stem elongation occurs during night. The growth process has a temperature coefficient $Q_{10}>2$, its optimum lies around 30°. The rate of food translocation, however, has a temperature coefficient $Q_{10}<1$, so that at higher nyctotemperatures, less sugar reaches the growing region, and the food supply becomes limiting. Thus in young small tomato plants, where food translocation takes place over short distances only, the optimal nyctotemperature coincides with the optimal temperature of the growth process (30°). As the tomato plant becomes taller, and the assimilating and growing regions become separated by longer distances, the food translocation becomes more and more limiting at the higher temperatures so that the optimal nyctotemperature drops to lower and lower levels (13-18°) in different tomato varieties. This same phenomenon can be seen in LAURIE and KIPLINGER's data on page 155 for orchids. Seedlings must be kept 4-10° warmer than mature plants. This is also the reason why in spring so many garden crops and flowers are germinated in greenhouses, where they are kept warm. By the time that their temperature requirements have been lowered, the outside temperatures have sufficiently risen to insure good growth of the seedlings when brought into the open.

The shift in optimal photo- and nyctotemperature according to the light intensity during the photoperiod, which was found in the tomato experiments in the air-conditioned greenhouses is well known in commercial practice, as indicated previously. In future work a further differentiation of the nyctotemperature effect must be made, and a more precise localization of the temperature effect has to be achieved.

The seeds of many plants germinate well only when they are subjected to a daily fluctuation in temperature (HARRINGTON 1923). This does not seem to be a case of thermoperiodicity in the sense that processes with different optimal temperatures have to alternate to cause germination. This is perhaps best demonstrated by the experiments of MORINAGA (1926) who found that seeds of *Cynodon dactylon* require alternation of temperature for best germination, but that scarification for 3-9 minutes with concentrated sulphuric acid made optimal germination possible without alternation of temperature. TOOLE (1940) found the same effect for *Oryzopsis*. It is also demonstrated by the fact that not the actual temperatures employed, but the alternation of temperatures as such determine germination (HARRINGTON 1923). Therefore the seat of response to alternating temperatures seems to be in the seed coat and not in the embryo. The alternating temperatures seem to affect the "encasing structures interfering with oxygen absorption by the embryo and perhaps carbon dioxide elimination from it, resulting in the limitation of the processes dependent upon these" (case 4 of CROCKER 1916). This conclusion differs from the one reached by MORINAGA (1926), who concluded that "alternating temperatures have their effects on the embryos."

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SPECIAL SUPPLEMENTS

Special Supplement 1

STUDIEN ÜBER PHOTOPERIODIZITÄT IN DEN TROPEN*

von

ERWIN BÜNNING

Botanisches Institut der Universität, Tübingen

Von Juni 1938 bis zum Juli 1939 unternahm ich im Auftrage des Reichsforschungsrats und des Forschungsdienstes eine Reise nach Java und Sumatra, um dort vor allem über Fragen der Tagesperiodizität bei Pflanzen zu arbeiten. Da ich gleich nach der Rückkehr von meiner Reise einberufen wurde, war es mir bisher nicht möglich, über die Ergebnisse zu berichten. Inzwischen sind jedoch einige Arbeiten erschienen, deren Resultate sich weitgehend mit meinen berühren. So möchte ich hier, um eine Doppelbearbeitung zu vermeiden, wenigstens kurz über meine Arbeit berichten. Dabei berücksichtige ich auch Versuche, die schon in den vorhergehenden Jahren in Deutschland ausgeführt wurden. Ich hoffe, nach Kriegsschluss eine ausführliche Bearbeitung vorlegen zu können.

Die Resultate wurden zum Teil durch Laboratoriumsversuche, zum Teil durch Freilandbeobachtungen gewonnen. Zu letzteren hatte ich während ausgedehnter Reisen in dem grossen Gebiet zwischen Ostjava und Nordwestsumatra sowohl auf Pflanzungen wie in der freien Natur genügend Gelegenheit. Dabei wurde auch reichlich Samenmaterial gesammelt, das der weiteren Fortsetzung der Untersuchungen dienen sollte, jedoch durch die Kriegsumstände zum Teil nicht mehr nach Deutschland gelangte, zum Teil durch Nichtbearbeitung wertlos geworden ist.

Photoperiodische Untersuchungen an tropischen Pflanzen sind, abgesehen von der praktischen Bedeutung ihrer Anwendung auf tropische Kulturpflanzen, insofern lohnend, als die extremen Bedingungen in den Tropen, kurzer Tag, schroffer Übergang von Hell zu Dunkel, sowie vor allem das photoperiodische Angepasstsein der Pflanzen an diese Klimaeigentümlichkeiten, die Klärung mancher Fragen erheblich erleichtern. Es scheint sogar, dass viele tropischen Pflanzen infolge des genannten Angepasstseins für photoperiodische Reize viel empfindlicher sind als die Pflanzen unserer Breiten. Das ergibt sich schon aus mehreren Angaben in der Literatur. Ich erwähne nur die Arbeit KUILMANS, aus der hervorgeht, dass die geringen jahresperiodischen Schwankungen der Tageslänge in den Tropen genügen, um beim Reis starke photoperiodische Reaktionen auftreten zu lassen, die bei der Auswahl des Saatguts für die einzelnen Anbaugebiete Berücksichtigung erfordern.

Auch in der freien Natur fand ich zahlreiche Beispiele dafür, dass selbst dort, wo, abgesehen eben von den geringen Schwankungen in der Tages-

* This interesting article on diurnal rhythm in plants has been reprinted, with the author's permission from Forschungsdienst (Neudamm) 10: 550-553, 1940.

länge, das Klima praktisch während des ganzen Jahres gleichmässig bleibt, eine ausgeprägte Jahresperiodizität des Blühens auftreten kann.

Die bisherigen Versuche zur Erklärung des Photoperiodismus bestehen vor allem im Studium der Beeinflussung der chemischen Zusammensetzung durch den photoperiodischen Reiz (Mengenverhältnis von Kohlehydraten und Stickstoff, Fermentgehalt, Blühhormonbildung). Ich habe 1936 auf Grund von Versuchen mit *Phaseolus* die Ansicht begründet, dass die photoperiodischen Reaktionen entstehen, weil die Pflanze aus inneren Ursachen einen tagesperiodischen Wechsel ihres inneren Zustandes durchmacht, und ein Lichtreiz einen ganz verschiedenartigen Einfluss auf die Pflanze ausübt, je nachdem, ob er in der Morgen oder in der Abendphase dieser endogenen Rhythmik einwirkt. Im ersteren Falle fördert, im zweiten hemmt er die reproduktive Entwicklung. Diese endogene Tagesrhythmik selber, die somit als die Grundlage für die Möglichkeit photoperiodischer Reaktionen betrachtet wird, war schon aus Studien über tagesperiodische Vorgänge an der Pflanze, namentlich durch die Analyse von Blattbewegungen bekannt geworden.

Meine Auffassung hat inzwischen durch die Versuche Lindenbeins an Tomaten sowie an *Phaseolus vulgaris* und *multiflorus* ihre Bestätigung gefunden. Ich selber habe zu dieser Frage Beobachtungen an tropischen Kulturpflanzen durchführen und meine Auffassung ebenfalls bestätigen können. Aus dem Studium der Blattbewegungen ergab sich, dass viele tropische Pflanzen (durchweg zum Kurztagtyp gehörend) eine relativ lange Abendphase der endogenen Rhythmik besitzen und die tägliche Beleuchtungsdauer auf 6 bis 10 Stunden abgekürzt werden muss, um zu verhindern, dass das Licht noch während der Abendphase der inneren Rhythmik auf die Pflanze einwirkt und dadurch die reproduktive Entwicklung hemmt. Noch weitere Abkürzung der Beleuchtungsdauer ist bedeutungslos. So lange eine Beleuchtung während der (durch die Blattbewegung angezeigten) Abendphase der endogenen Rhythmik vermieden wird, hemmt das Licht in keiner Weise die reproduktive Entwicklung.

Um das Wesen der photoperiodischen Reizwirkung näher verstehen zu können, ist naturgemäss zunächst eine Analyse der endogenen Rhythmik selber erforderlich, d. h., es ist der Mechanismus der physiologischen Selbststeuererung im Wechsel der beiden Phasen dieser Rhythmik zu klären. Ich habe hierzu vor allem *Nicotiana tabacum, Phaseolus multiflorus* und *Nymphaea lotus* näher untersucht. Bei *Phaseolus* konnte schon früher (1935) ermittelt werden, dass ein wesentlicher Teil der inneren Rhythmik in einem Wechsel des Säuregrades besteht, und hierfür tagesperiodische Schwankungen der Kohlensäureproduktion entscheidend sind. Mosebach hat dieses Ergebnis inzwischen bestätigt. *Nymphaea* verhält sich ähnlich. Der *p*H-Wert beträgt hier morgens etwa 4,5, abends 4,3. Die tagesperiodischen Schwankungen der Kohlendioxydproduktion (sowie auch des Sauerstoffverbrauchs) sind unerwartet hoch, und stehen in sehr enger Beziehung zu dem durch die Krontblattbewegungen angezeigten Wechsel von Morgen- und Abendphase der inneren Rhythmik. Die Kohlendioxydabgabe steigt abends, genau zu dem Zeitpunkt, in dem sich die Blüte öffnet, um 100 bis 150%, morgens sinkt sie wieder. Das trifft sowohl für Pflanzen zu, die dem normalen Licht-Dunkel-Wechsel ausge-

setzt sind, als auch für solche, die ihre endogene Rhythmik in der Dunkelkammer fortsetzen.

Auch *Nicotiana* weist abends eine erhöhte Kohlendioxydproduktion auf, die jedoch nicht zur Ansäuerung des Zellsaftes führt, sondern im Gegenteil zu dessen Absäuerung, da sie mit einem Abbau von Oxal- und Apfelsäure einhergeht (vgl. die Untersuchungen SCHWARZES am gleichen Objekt).

Nebenher bemerke ich, dass die Aziditätsänderungen in allen Fällen zur Erklärung der Blattbewegungen genügen. Experimentell durch Übertragung der entsprechenden Pflanzenteile in Lösungen abgestufter Azidität hervorgerufene Änderungen des Säuregrades in den Zellen lösen die entsprechenden Bewegungen aus. Diese werden übrigens möglich, weil das Wachstum von Ober- und Unterseite der Blätter bzw. Blattstiele zwar in ähnlicher Weise von der Azidität abhängt, aber die für das Wachstum optimalen *p*H-Werte beider Seiten als Ausdruck der physiologischen Dorsiventralität etwas voneinander verschieden sind. Die in diesem Zusammenhang ausgeführten Untersuchungen über die *p*H-Abhängigkeit des Wachstums ergaben übrigens, wie ebenfalls nebenher bemerkt sei, dass ganz gering erscheinende Schwankungen der Azidität einen überaus starken Einfluss auf das Wachstum haben können. Bei bestimmten Geweben der *Nymphaea lotus* ist das Wachstum bei *p*H 4,5 gleich Null, es steigt bei *p*H 4,3 zu einem starken, bei *p*H 4,8 zu einem schwächeren Maximum, um bei noch extremeren Werten schnell wieder abzusinken.

Als nächste Ursache der Stoffwechselschwankungen wurde ein Wechsel der Enzymtätigkeit, namentlich der Diastasetätigkeit erkannt. Die Diastasetätigkeit ist abends grösser als morgens, so dass abends mehr Zucker zur Atmung geliefert wird. Das Ausmass der Aktivitätssteigerung beträgt z. B. bei *Phaseolus* 50 bis 100%.

An diesem Punkt berühren sich meine Untersuchungen auch mit den Studien SPEIDELS über das Bluten der Pflanzen. SPEIDEL kommt zur Ansicht, dass das Bluten durch eine Arbeitsleistung der lebenden Zellen möglich wird, für die die Atmung erforderlich ist. Zur Erklärung der tagesperiodischen Schwankungen der Blutungsintensität verweist SPEIDEL auf zwei Möglichkeiten: Schwankungen der Zufuhr von Atmungsmaterial und rhythmischer Wechsel der Enzymaktivität.

Ich bemühte mich lange Zeit vergeblich, tagesperiodische Schwankungen im Kolloidzustand des Plasmas zu finden, die man als Ursache für die Schwankungen der Enzymaktivität verantwortlich machen könnte. Hingegen fand ich, dass eine klare Beziehung zwischen dem Kolloidzustand der Chloroplasten und der Diastaseaktivität besteht. Kürzlich erschien eine Mitteilung von KROSSING, die mir dieses zunächst nicht erwartete Ergebnis durchaus verständlich macht, er fand nämlich beim Spinat, dass von den verschiedenen Zellinhaltsteilen nur die Chloroplastensubstanz amylatisch wirksam ist. Auch auf die Untersuchung STOPPELS über die Bedeutung des Chlorophylls für die Blattbewegungen sei verwiesen.

Die Chloroplasten fand ich in der Morgenphase der endogenen Rhythmik flach und mit unregelmässiger Oberfläche, mikroskopisch nicht homogen, oft deutliche Entmischungen zeigend, in der Abendphase dagegen kugelig glatt und homogen. Über ähnliche Beobachtungen haben schon andere Autoren berichtet. Auch diese Veränderungen vollziehen sich sowohl im normalen Licht-Dunkel-Wechsel als auch in der Dunkelkammer.

Die unterschiedliche Chloroplastenbeschaffenheit lässt sich durch Übertragung der Gewebe in Lösungen verschiedener Azidität auch experimentell leicht hervorrufen.

Meine Hauptarbeit bestand in der weiteren Analyse dieser einzelnen Erscheinungen. Dabei wurde folgendes, in der ausführlichen Darstellung der Versuche näher zu begründendes Bild von der physiologischen Selbststeuerung der Vorgänge gewonnen. Der beim normalen Licht-Dunkel-Wechsel nachmittags, in der Dunkelkammer während der Abendphase der endogenen Rhythmik herrschende Kolloidzustand der Chloroplasten ist mit einer Freisetzung von Amylase aus einer adsorptiven Bindung verknüpft; in den Chloroplasten wird Stärke abgebaut, Zucker gebildet und die Kohlendioxydproduktion gefördert. Die Kohlensäureanreicherung und Aziditätsänderung ist für mehrere physiologische Vorgänge, namentlich für die Wachstumsintensität, wichtig. In den Chloroplasten steigt die Kohlensäurekonzentration nur langsam, jedenfalls macht sie sich erst spät bemerkbar; sie führt dann zum Umschlagen des Kolloidzustandes, wobei Amylase absorptiv gebunden wird und die Zuckerproduktion sowie die Kohlensäurekonzentration allmählich wieder sinken, bis nach einem weiteren Halbtag wieder der erstgenannte Kolloidzustand erreicht wird. Das Licht kann in den Gang dieser endogenen Rhythmik entscheidend eingreifen, weil es selber die Kohlensäurekonzentration durch Einschaltung der Assimilation vermindert.

Die tiefgreifende Verschiedenheit der Chloroplastenbeschaffenheit in den beiden Phasen der endogenen Rhythmik lässt es verständlich erscheinen, dass das Licht einen verschiedenartigen Einfluss auf die Pflanze ausübt, je nachdem in welcher Phase der inneren Rhythmik es einwirkt. Die für mehrere photoperiodische Reizwirkungen konstatierte Parallelität zwischen der unterschiedlichen Wirksamkeit verschiedener Spektralbereiche und deren Absorption im Chlorophyll ist in diesem Zusammenhang bemerkenswert.

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Nachtrag zu den "Studien über Photoperiodizität in den Tropen":— Inzwischen sind ausführlichere Veröffentlichungen der Ergebnisse erschienen (vgl. das Literaturverzeichnis). Vielleicht ist hier auch ein Hinweis auf einige praktische Anwendungen angebracht.

In vielen Teilen Javas und Sumatras, vor allem auch auf der Karohochfläche in Nord-Sumatra hatte ich reichlich Gelegenheit, den Gemüseanbau zu beobachten. Dieser Anbau hat (selbst für den Export, z. B. zur malaiischen Halbinsel) vor dem Krieg eine erhebliche Bedeutung erlangt. Die Samen für diesen Gemüseanbau mussten zum grossen Teil regelmässig importiert werden, da diese europäischen Gemüsepflanzen unter den tropischen Bedingungen nicht oder nur sehr spärlich blühen. Dadurch ist es unmöglich geworden, an diesen Pflanzen eine Züchtungsarbeit in den Tropen vorzunehmen. Eine Züchtungsarbeit wäre aber z.B. schon darum sehr notwendig, weil zahlreiche Krankheiten erhebliche Ausfälle bedingen. Der Grund für das Ausbleiben der Blütenbildung liegt natürlich im Langtagcharakter der genannten Pflanzen. Zwar würden die meisten dieser Gemüsearten in den gemässigten Zonen noch im 12-Stunden-Tag, also bei der in den Tropen gegebenen Beleuchtungsdauer, zur Blüte kommen; aber wenn die hohe Temperatur der Tropen zum kurzen Tag hinzukommt, wird die "kritische Tageslänge" so sehr heraufgesetzt, dass zur Blütenbildung mehr als 12 Stunden Licht je Tag notwendig sind. Diese von LANG und MELCHERS an *Hyoscyamus* ermittelte Temperaturabhängigkeit der kritischen Tageslänge gilt anscheinend allgemein. Jedenfalls sieht man in den Tropen, dass die Langtagpflanzen in grösserer Höhe, also bei niedrigerer Temperatur gut blühen. (Hieraus erklärt sich auch die von VAN STEENIS hervorgehobene Tatsache, dass Pflanzen gemässigter Zonen in den malaiischen Gebirgen in grösserer Höhe gut gedeihen, während sie in der Ebene nicht blühen). Mann könnte nun, um von jenen Gemüsepflanzen Samen zu gewinnen, versuchen, die Tageslänge durch künstliches Licht um 1-2 Stunden zu verlängern. Das wäre jedoch zu kostspielig. Nach den jetzt vorliegenden Erkenntnissen genügt es aber, wenn während der Nacht zu einem bestimmten Zeitpunkt, der sich aus dem Studium der endonomen Rhythmik der Pflanze leicht ergibt, noch ein schwaches und kurzes Zusatzlicht geboten wird. Das Problem der Saatgewinnung und der Züchtungsarbeit an Gemüsepflanzen europäischer Herkunft in den Tropen lässt sich also wohl lösen.

Noch in anderer Hinsicht ist eine Anwendung der Ergebnisse für die tropische Landwirtschaft wohl möglich. Es gibt einige Pflanzen, die zwar Kurztagpflanzen sind, die aber bei den in den Tropen gegebenen extremen Kurztagbedingungen doch nicht ihre optimale Entwicklung zeigen. Das gilt z.B. für *Perilla* und *Soja*. Beide gedeihen bekanntlich in der gemässigten und subtropischen Region Ostasiens sehr gut. Werden die dort heimischen Sorten in den Tropen angebaut, so kommen sie infolge des kurzen Tages so schnell zum Blühen, dass die vegetative Entwicklung zu gering bleibt, z.B. kann *Soja* dann schon nach einem Monat blühen, während die Pflanzen erst 10 cm hoch sind. Auch bei mehreren Reis-

sorten, die man aus gemässigteren Gegenden in die Tropen einführen wollte, hat sich dieser Übelstand gezeigt. Wie nützlich es wäre, hier einen Ausweg zu finden, ergibt sich aus den geringen ha-Erträgen an *Soja* in Java. Auf Java betrug der Ertrag je ha vor dem Krieg nur etwa 600 kg, während in der Mandschurei etwa 2000 kg je ha geerntet werden. Eine Verbesserung der Sojaernten auf Java und in anderen äquatornahen Gebieten könnte durch Berücksichtigung der photoperiodischen Eigenschaften gelingen. Hierzu müssten die extremen Kurztagbedingungen gemildert werden. Auch das wäre wieder zu kostspielig, wollte man die Tageslängen durch künstliches Licht um 1-2 Stunden verlängern. Jetzt wissen wir, dass es nur erforderlich ist, im richtigen Zeitpunkt der Nacht ein kurzdauerndes schwaches Zusatzlicht zu bieten. Eine Beleuchtungsdauer von wenigen Minuten je Nacht würde, einige Tage hindurch geboten, genügen, um die vegetative Entwicklung auf das wünschenswerte Mass zu steigern. Es kommt nur darauf an, das Ergänzungslicht genau im günstigsten Zeitpunkt der Nacht zu bieten. Da wir aber die jeweilige Reaktionsbereitschaft jetzt aus dem Studium der Blattbewegungen leicht erkennen können, bedeutet die Ermittlung dieses Zeitpunktes keine Schwierigkeit.

Hier sollten nur grundsätzlich mögliche Wege gezeigt werden. Das Weitere müssen Versuche an Ort und Stelle ergeben.

E. B.

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Special Supplement 2

DIE ENTWICKLUNGSPHYSIOLOGISCHE BEDEUTUNG DER ENDOGENEN TAGESRHYTHMIK BEI DEN PFLANZEN*

von

ERWIN BÜNNING

Botanisches Institut der Universität, Tübingen

HARDER hat kürzlich in dieser Zeitschrift die mannigfaltigen photoperiodischen Erscheinungen, vor allem auf Grund seiner Versuche an *Kalanchoë*, beschrieben. Auf die Theorien zur Erklärung dieser merkwürdigen Abhängigkeit der pflanzlichen Entwicklung von der Rhythmik des Licht-Dunkel-Wechsels ist HARDER absichtlich nicht eingegangen.

Man hatte schon mehrfach geglaubt, brauchbare Erklärungen gefunden zu haben, aber dann wurden wieder die überraschendsten Tatsachen Entdeckt, die das Problem nur verworrener erscheinen liessen. Für den Einfluss des Lichtes auf die Blütenbildung ist, wie schon frühzeitig erkannt wurde, nicht nur nicht die gebotene Lichtmenge, sondern auch nicht etwa die tägliche Dauer von Licht oder von Dunkelheit ausschlaggebend. Aber auch das Längenverhältnis von Licht- und Dunkelperiode ist nicht entscheidend (beispielsweise wirkt ein Licht-Dunkel-Wechsel von 8: 16 Stunden nicht ebenso wie ein Wechsel von 12: 24 Stunden).

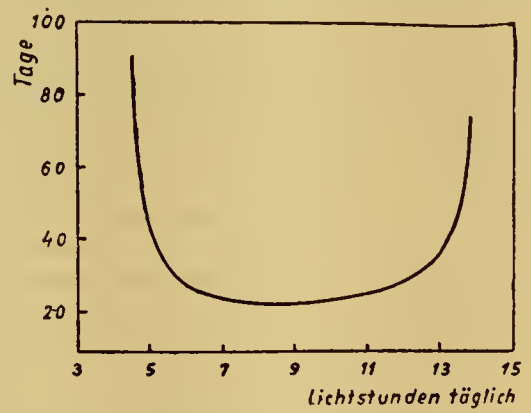

FIG. 1. — Photoperiodische Reaktion einer Kurztagpflanze (*Chrysanthemum*), konstruiert von LANG und MELCHERS nach Versuchen MOŠKOVS. Eine Lichtperiode von etwa 7-11 Stunden täglich wirkt optimal auf die Blütenbildung. Oberhalb von etwa 14, und unterhalb von etwa 5 Stunden erfolgt überhaupt keine Blütenbildung mehr.

* Eine Ergänzung zum Artikel R. HARDER (Naturwiss. 33: 41, 1946). — Reprinted, with the author's permission, from Naturwissenschaften 33: 271-274 (Nov. 15, 1946).

Sofern die experimentell gebotenen Licht-Dunkel-Rhythmen noch den in der freien Natur möglichen entsprechen, d.h. solange die Summe von Licht- und Dunkelperiode 24 Stunden beträgt und innerhalb dieser Zeit nur eine Licht- und nur eine Dunkelperiode geboten wird, lässt sich das Verhalten von Kurz- und Langtagpflanzen durch die Kurven der Fig. 1 und 2 kennzeichnen. Gehen wir aber von diesen normalen Bedingungen ab, so werden die Verhältnisse immer verwickelter und rätselhafter. In der neueren Literatur findet sich eine Fülle von Zahlenmaterial über die Wirkung verschiedenartig zusammengesetzter Licht-Dunkel-Rhythmen, das der Zusammenfassung zu einer einheitlichen Theorie trotzte.

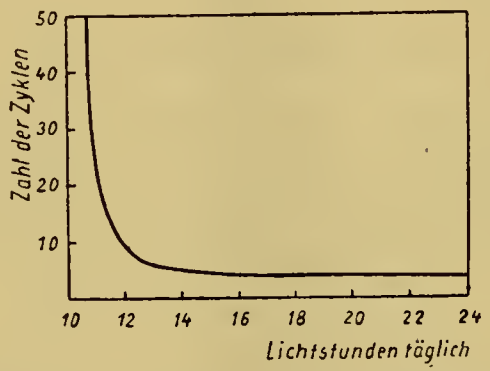

Fig. 2. — Photoperiodische Reaktion einer Langtagpflanze (*Hyoscyamus niger*) nach Lang und Melchers. Die Ordinate gibt an, wieviel Zyklen mit den in der Abszisse genannten Tageslängen geboten werden müssen, um die Blütenbildung auszulösen. Je mehr die kritische Tageslänge von 11 Stunden überschritten wird, um so leichter folgt Blütenbildung.

Ich habe mich seit 1935 bemüht, eine solche Theorie zu finden und zu begründen, nämlich zu zeigen, dass sich die photoperiodischen Reaktionen aus dem Wechselspiel einer endonomen Tagesperiodizität der Pflanze mit dem gebotenen Licht-Dunkel-Rhythmus erklären. Wenn ich hier gemäss einer Aufforderung der Schriftleitung den gegenwärtigen Stand der Theorie darstelle, darf ich nicht versäumen, zu betonen, dass ich erst durch die wiederholte Erörterung der Fragen mit den Herren Lang und Melchers vom Kaiser Wilhelm-Institut für Biologie dazu gekommen bin, die entscheidenden Untersuchungen zur Begründung der Theorie durchzuführen. Unsere Auffassungen standen sich ursprünglich, wie es schien, unvereinbar gegenüber. Allmählich aber hat sich gezeigt, dass sich alle Befunde recht gut zu einem einheitlichen Bild vereinigen lassen. Dazu hat namentlich auch noch die unter der Leitung von Melchers durchgeführte Arbeit von Fräulein Claes beigetragen. Die Arbeiten von Melchers und Mitarbeitern gehen vom allgemeinen Problem der Blütenbildung aus, meine eigenen vom Problem der Bedeutung der endogenen Rhythmik für die Entwicklung der Pflanze. Diesem Ausgangspunkt entsprechend soll auch die folgende Darstellung eingeengt bleiben, d.h., es soll wohl gezeigt werden, dass diese endogene Rhythmik für die photoperiodische Beeinflussung der Blütenbildung wichtig ist; aber auf die Frage, welche Vorgänge, z.B. welche zur Blütenbildung führenden Prozesse es sind, die hier modifiziert

werden, soll nicht eingegangen werden. Der angeführte Aufsatz HARDERS sowie die Arbeiten von MELCHERS und Mitarbeitern enthalten namentlich durch ihre Verbindung zur Blühhormonforschung wichtige Beiträge und Literaturangaben zu dieser anderen Frage.

Die Endogene Tagesrhythmik:— Bei höheren Pflanzen ist an sehr verschiedenen physiologischen Vorgängen eine endogene Tagesrhythmik erkennbar, d.h. diese Vorgänge zeigen auch bei konstanten Aussenbedingungen tagesperiodische Schwankungen. Die endonome Natur der Schwankungen wird namentlich dadurch gegen alle Zweifel erwiesen, dass sie nicht an die Tageszeit gebunden zu sein brauchen, und dass sie auch nicht genau die 24-Stunden-Rhythmik einhalten müssen. Selbst im Thermostaten verwahrte isolierte Organe zeigen noch diese innere Rhythmik. Bei vielen Pflanzen führt die endogene Rhythmik auch zu endogenen tagesperiodischen Blattbewegungen, und an diesem Vorgang lässt sich der zeitliche Verlauf der Rhythmik natürlich viel leichter verfolgen als an den von ihr gesteuerten Zellvorgängen.

Von den beiden Phasen der inneren Rhythmik ist die eine dem normalen Tag, also der Lichtperiode, angepasst, die andere der Dunkelperiode. Erstere habe ich die photophile, letztere die skotophile Phase genannt.

Die photophile Phase der endogenen Rhythmik zeichnet sich durch folgende Eigentümlichkeiten aus: hohe synthetische Leistungsfähigkeit, z. B. starke Syntheseleistungen der Hydrolasen und starke assimilatorische Fähigkeit, geringe Atmung und dementsprechend oft verminderte Azidität. In der skotophilen Phase hingegen ist die hydrolytische Leistungsfähigkeit gesteigert, Stärke und Zucker werden verstärkt abgebaut, die Atmung ist erhöht und infolgedessen oft auch die Azidität. Der autonome Wechsel zwischen beiden Phasen erklärt sich daraus, dass während der photophilen Phase durch die Stoffwechselverschiebung, namentlich durch die Aziditätsverminderung, allmählich ein Plasmazustand geschaffen wird, der zwangsläufig die skotophile Phase eintreten lässt. Besteht diese aber wieder eine Zeitlang, so wird durch die Aziditätserhöhung oder vielleicht auch noch durch andere Stoffwechseländerungen schliesslich wieder zwangsläufig der für die Syntheseleistungen günstige Plasmazustand geschaffen.

Als notwendige Folge dieser plasmatischen Veränderungen treten auch die übrigen tagesperiodischen Schwankungen in physiologischen Erscheinungen auf, z.B. die Schwankungen in der Permeabilität und im Wachstum. Es bereitet auch keine Schwierigkeit, aus den genannten Veränderungen die Notwendigkeit der tagesperiodischen Blattbewegungen abzuleiten. Aber diese Frage braucht uns hier nicht zu interessieren.

Die beiden Phasen lösen einander nicht sprunghaft ab, die photophile Phase steigt allmählich immer mehr zu ihrem Maximum (d.h. zu einem Extremwert der genannten Eigentümlichkeiten) an, dann klingt sie allmählich ab und wird durch die ebenfalls allmählich einsetzende skotophile Phase abgelöst, die auch langsam ihr Maximum erreicht und übersteigt.

Der Phasenwechsel erfolgt zwar endogen, aber äussere Reize wirken doch stark regulierend. So kann durch kurzdauernde äussere Anstösse bestimmt werden, zu welchem Zeitpunkt die Phasen der inneren Rhythmik auftreten. Wirksame Reize sind dabei z.B. die Temperatur und namentlich das Licht. Ausserdem wird durch den tagesperiodischen Wechsel von

äusseren Faktoren, namentlich wieder durch den tagesperiodischen Licht-Dunkel-Wechsel, erreicht, dass die endogene Rhythmik genau die 24-Stunden-Periode einhält, von der sie bei konstanten Aussenbedingungen etwas abweichen kann.

Weitere wichtige Eigentümlichkeiten der beiden Phasen sind noch die, die zu ihrer Bezeichnung geführt haben: Licht wirkt in der photophilen Phase fördernd, in der skotophilen hemmend auf die Blütenbildung.

Beim Wechselspiel der endogenen Rhythmik mit dem gegebenen Licht-Dunkel-Wechsel ist also zweierlei zu beachten. Einerseits die zeitliche Einregulierung der Phasen, andererseits die fördende bzw. hemmende Wirkung in den Phasen selber.

Die Zeitliche Einregulierung der Phasen durch das Licht:— Die bei der Phasenregulierung durch das Licht geltenden Gesetze sind uns namentlich durch das Studium der Blattbewegungen bei den verschiedenartigen Licht-Dunkel-Rhythmen gut bekannt beworden. Ich will nur das Verhalten bei Licht-Dunkel-Rhythmen darstellen, die sich dem normalen 24-Stunden-Rhythmus einfügen.

Es ist nicht etwa so, dass beim Beginn eines Lichtreizes sofort eine bestimmte Phase der endogenen Rhythmik einsetzt, sondern es verstreicht eine gewisse, für die betr. Pflanze charakteristische Reaktionszeit, bis die Phase beginnt.

Bei manchen Pflanzen setzt die photophile Phase schon sehr schnell nach dem Beginn des Lichtreizes ein. Es sind das hauptsächlich die Pflanzen tropischer und subtropischer Herkunft. Wie lange Zeit der regulierende Lichtreiz einwirkt, ob mehrere Stunden oder nur wenige Minuten, ist dabei ziemlich belanglos. Fig. 3 zeigt das Verhalten dieses Typs A. In

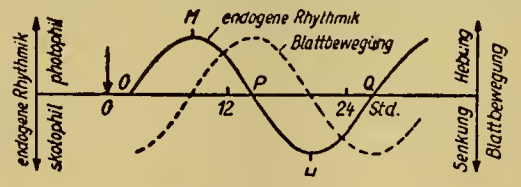

Fig. 3. — Regulierung einer endogenen Rhythmik und der Blattbewegung durch einen Lichtreiz bei Kurztagpflanzen. Pfeil: Beginn des Lichtreizes. Weitere Erklärung im Text.

der Abbildung ist nicht nur das An- und Absteigen von photophiler und skotophiler Phase eingezeichnet, sondern auch das Heben und Senken der Blätter, weil dieses ein so wichtiger Anzeiger für den jeweiligen Zustand der inneren Rhythmik ist. Wir sehen, dass sich die Blätter heben, solange sich die Pflanze in der photophilen Phase befindet und senken, sobald die skotophile Phase einsetzt. Die maximale Hebungsgeschwindigkeit fällt mit dem Maximum der photophilen, die maximale Senkungsgeschwindigkeit mit dem Maximum der skotophilen Phase zusammen.

Bei anderen Pflanzen, fast ausschliesslich solchen aus den gemässigten und polaren Regionen, tritt die photophile Phase erst mehrere Stunden, oft 10-12 Stunden nach Beleuchtungsbeginn ein, auch dabei ist die Zeitdauer des regulierenden Lichtreizes wieder ziemlich belanglos. Das Verhalten dieses Typs B zeigt uns Fig. 4.

Es scheint, dass bei allen Pflanzen, einerlei zu welchem der beiden Typen sie gehören, die photophile Phase sich in einer Blatthebung die skotophile in einer Blattsenkung zu erkennen gibt. Die Möglichkeit von Ausnahmen muss offenbleiben.

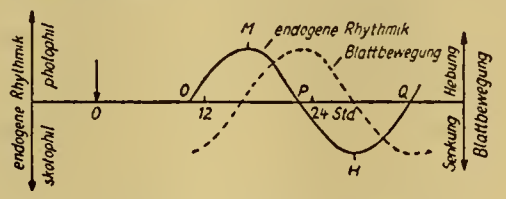

Fig. 4. — Wie Fig. 3, jedoch für Langtagpflanzen.

Ob es zwischen beiden Typen Übergänge gibt oder ob noch andersartige Typen existieren, wollen wir hier nicht untersuchen.

Nun hat sich gezeigt, dass der erstgenannte Typ identisch ist mit dem Kurztagtyp, der zweite mit dem Langtagtyp. Wenn sich die genannte Regel, dass die Blatthebung unabhängig vom Typ die photophile Phase anzeigt, allgemein bestätigen sollte, wäre hier ein einfaches Hilfsmittel zur schnellen Unterscheidung von Kurz- und Langtagpflanzen gefunden.

Fördernde und Hemmende Lichtwirkung in den Phasen der Endogenen Rhythmik:— Nun fällt es uns nicht mehr schwer, die photoperiodischen Erscheinungen zu verstehen.

Typ A (*Kurztagpflanze*). — Der von dem Zeitpunkt des Pfeils (Fig. 3) an einwirkende Lichtreiz muss die Blütenbildung fördern, weil er ja sofort oder sehr bald in die (von ihm selber einregulierte) photophile Phase fällt. Die Förderung wird um so grösser, je länger das Licht einwirkt (wie es nach Fig. 1 auch sein muss). Wirkt das Licht aber länger als bis zum Punkt P, so macht sich eine Hemmung bemerkbar, die um so stärker werden muss, je weiter der Lichtreiz sich über diesen Zeitpunkt hinaus ausdehnt (auch das bestätigen uns die in Fig. 1 dargestellten experimentellen Befunde). Dieses Hemmlicht braucht nicht mit der ersten, die Phasen einregulierenden Lichtperiode zusammenhängend geboten zu werden. Wir können es auch als eine zweite Lichtperiode gesondert darbieten, und diese zweite Lichtperiode braucht nur kurz zu sein; die zweite Phase der inneren Rhythmik ist so skotophil, dass selbst kurze Lichtblitze zur Hemmung genügen, so dass die Kurztagpflanze dann im Kurztag nicht blüht! Ein zur ersten einregulierenden Lichtperiode zusätzlich gebotener zweiter Lichtreiz hemmt die Blütenbildung naturgemäss dann am stärksten, wenn er im Zeitpunkt H geboten wird (wo die skotophile Phase ihren Extremwert erreicht hat). Diese Konsequenzen finden sich in Arbeiten von Hamner und Rasumov, am deutlichsten in Versuchen von Harder und Bode völlig bestätigt (vgl. Fig. 5). Die Kurztagpflanze kann so selbst im Kurztag am Blühen verhindert werden.

Lassen wir das zweite Licht erst einwirken, nachdem die innere Rhythmik den Punkt Q durchschritten hat, so zeigt sich, dass der zweite Lichtreiz nicht mehr hemmend wirkt, sondern, wie es nach der Theorie sein muss, wieder fördert (Snyder, vgl. Bünning)!

Typ B (*Langtagpflanze*). — Der vom Zeitpunkt des Pfeils (Fig. 4) an einwirkende Lichtreiz fällt zunächst nicht in die photophile Phase, die er selber einreguliert, erst wenn wir den Lichtreiz bis über den Punkt O hinaus ausdehnen, wird die Blütenbildung gefördert, und zwar umso mehr, je länger das Licht einwirkt. (Diese theoretische Förderung entspricht wieder den in Fig. 2 dargestellten experimentellen Befunden.)

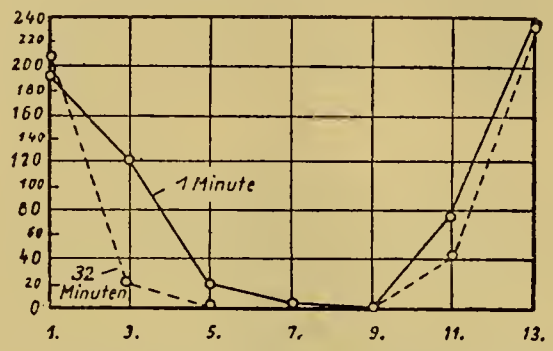

Fig. 5. — Wirkung eines während der Dunkelphase gebotenen Zusatzlichtes auf die Blütenbildung der Kurztagpflanze *Kalanchoë blossfeldiana*. Das Zusatzlicht dauerte 1 bzw. 32 Minuten. Man sieht, dass das Zusatzlicht die Blütenbildung am meisten unterdrückt, wenn es in der 7. bis 9. Stunde der Dunkelperiode (d. h. etwa 17 Stunden nach Beginn der vorhergegangenen 9 stündigen Lichtperiode) wirkt. Nach Harder und Bode.

Wir müssen die Förderung aber auch erreichen können, wenn wir das regulierende Licht nur kurz einwirken lassen, dann aber dafür sorgen, dass später, wenn die photophile Phase selbsttätig eingetreten ist, also zwischen den Punkten O und P der Fig. 4, ein zweiter Lichtreiz wirkt. Diese Konsequenz, nach der die Langtagpflanze dann im Kurztag blüht, ist in Versuchen von Naylor und Rasumov bestätigt. Die Förderung durch den zweiten Lichtreiz (der nur kurz zu sein braucht) muss naturgemäss um so stärker sein, je mehr der zweite Reiz dem Zeitpunkt maximaler photophiler Phase, also dem Punkt M genähert ist. Diese Folgerung hat sich in eigenen Versuchen und vor allem in denen von Fräulein Claes sehr gut bestätigt gefunden. *Hyoscyamus niger,* der als Langtagpflanze normalerweise mindestens 11 Stunden Langtag benötigt, um Blütenanlagen zu bilden, blüht bei einer täglichen Gesamtlichtzeit von nur 6 Stunden, wenn das die Rhythmik einregulierende Licht von 5 Stunden durch einen zweiten, nur 1-stündigen Lichtreiz ergänzt wird, der in der Mitte der photophilen Phase geboten wird (Fig. 6).

Um nun die Parallelität mit den zu Typ A angeführten Beweisen zu vervollständigen, müsste noch gezeigt werden, dass die Phase photophilen Verhaltens nicht nur etwa ¾ Tag nach Beginn des ersten Lichtreizes ein Maximum aufweist, sondern dass während einer diesem ersten Lichtreiz folgenden längeren Dunkelheit nach abermals 24 Stunden (d. h. 1¾ Tage nach Beginn des ersten Lichtreizes, also hinter Punkt Q der Fig. 4) nochmals ein Maximum der photophilen Phase durchschritten wird. Lang, Melchers und Frl. Claes haben nach persönlicher Mitteilung einen solchen Versuch soeben mit positivem Erfolg durchgeführt!

Die Bedeutung des Phasenwechsels:— Ich habe hier nur einen Teil der an anderer Stelle veröffentlichten Beweise angeführt, glaube aber schon damit ausreichend nachgewiesen zu haben, dass sich die vorgeschlagene Erklärung der photoperiodischen Erscheinungen als unausweichlich herausgestellt hat. Umgekehrt wird uns jetzt auch begreiflich, wie sich die endogene Tagesrhythmik ohne eine "Einprägung" von aussen her, nämlich allein durch Selektion aus einer ursprünglich noch nicht genau der Aussenrhythmik angepassten Periodizität entwickeln konnte. Die endogene Tagesrhythmik hat eben wegen ihrer Bedeutung für den Photoperiodismus mit allen ihren Einzelheiten, mit ihrem besondern Verlauf und ihrer besonderen Regulierbarkeit, einen erheblichen Selektionswert.

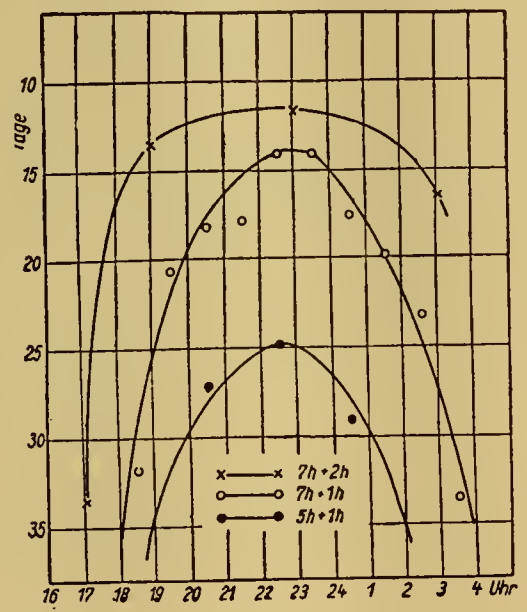

Fig. 6. — Die Langtagpflanze *Hyoscyamus niger* blüht, wenn zum Kurztag von 5-7 Stunden noch 1-2 Stunden Zusatzlicht während der Dunkelheit geboten werden. Die Hauptlichtperiode begann jeweils um 7 Uhr. Das Zusatzlicht fördert die Blütenbildung am stärksten, wenn es 16 Stunden nach Beginn jener ersten Lichtperiode geboten wird. Nach Claes.

Schon 1932 hatte ich aus dem Tatsachenmaterial die Schlussfolgerung abgeleitet, dass die Übereinstimmung der erblichen Tagesrhythmik mit der durch Aussenfaktoren bedingten möglicherweise für das Gedeihen der Pflanze wichtig sei. Durch die Analyse des Photoperiodismus ist uns die Bedeutung der endogenen Tagesrhythmik jetzt viel klarer geworden. Aber das Problem, warum die Pflanze regelmässig zwei Phasen mit ganz verschiedenen biochemischen Eigenschaften einander ablösen lässt, hat noch eine allgemeinere Bedeutung. Für die Leistungen der Pflanze beim Stoffaufbau, für die Bildung der einzelnen Hormone usw. genügt offenbar noch nicht die Arbeitsteilung zwischen den verschiedenen Zellen und Zellsorten. Es scheint vielmehr, dass bestimmte der für die zahlreichen Synthesen notwendigen Substanzen nur in verschiedenen Extremzuständen des Plasmas geschaffen werden können, in ein- und demselben Zustand vermag

die Zelle nicht alles zu leisten. Das muss der tiefere Sinn des regelmässigen Wechselns einer Phase hoher synthetischer und einer Phase hoher abbauender Fähigkeit sein. In der Pflanze sind gleichsam nicht nur mehrere Maschinen nebeneinander vorhanden, sondern diese Maschinen werden auch periodisch umkonstruiert, um allen Produktionsanforderungen gerecht werden zu können.

Wir können daher die Entwicklung nicht nur beeinflussen, indem wir die in der photophilen Phase ablaufenden Synthesen durch das dann gebotene Licht, also durch die dann eingeschaltete Photosynthese unterstützen, oder indem wir den in der skotophilen Phase ablaufenden Abbauvorgängen durch dann gebotenes Licht entgegenarbeiten, sondern wir können auch schon durch die blosse Hinderung der freien Entfaltung beider Phasen der endogenen Rhythmik eine Störung erreichen. Dieser Umstand ist offenbar mitbeteiligt bei der Unterdrückung der Blütenbildung durch einen Licht-Dunkel-Wechsel, der als Gesamtperiode schneller abläuft als es dem normalen Tag entspricht (z.B. durch einen 8: 8 stündigen Wechsel). Die durch solche Rhythmen bedingte Hemmung in der freien Entfaltung der Phasen der endogenen Rhythmik äussert sich deutlich in der starken Verminderung der Amplituden der Blattbewegungen.

Wenn schon diese freie Entfaltung der Phasen so wichtig ist, wird uns auch noch eine andere Beobachtung begreiflich. Nach persönlicher Mitteilung von Herrn Kollegen HARDER blüht *Kalanchoë* schon bei einer Beleuchtung von täglich einer Sekunde. Wir wissen aber schon lange auf Grund des Studiums der Blattbewegungen, dass die endonome Rhythmik durch so kurze Lichtblitze, die einmal je Tag geboten werden, zeitlich einreguliert und zur Erreichung der vollen Amplituden veranlasst werden kann.

Endlich können wir auf Grund dieser Überlegungen auch ohne weiteres verstehen, warum der bei Langtagpflanzen experimentell gebotene Zucker oder die experimentelle Hemmung der Atmung während der photophilen Phase (MELCHERS, LANG, CLAES) ebenso die Blütenbildung fördert, wie es das Licht in dieser Phase tut.

Literatur:—

(Nur die neuesten Arbeiten, aus denen die weitere Literatur entnommen werden kann, sind genannt.)

BÜNNING, E., Biol. Zbl. 64: 161, 1944. — BÜNNING, E., Fora 38: 93, 1944. — CLAES, H., Dissertation Tübingen, 1945. — HARDER, R., Naturwiss. 33: 41, 1946.

Special Supplement 3

BEITRÄGE ZUR GENETIK DES PHOTOPERIODISMUS*

I. Faktorenanalyse des Kurztagcharakters von Nicotiana tabacum "Maryland-Mammut"

von

A. LANG

Kaiser-Wilhelm-Institut für Biologie, Tübingen

Einleitung:— Bei der Bearbeitung von Fragen des Photoperiodismus kann, wie bei allen Problemen auf dem Gebiet der Entwicklungsphysiologie, die Analyse an zwei Punkten ansetzen, den beiden Endpunkten jeder entwicklungsphysiologischen Reaktionskette, Genotypus und Aussenmerkmal; das Endziel ist die vollständige Aufklärung dieser Reaktionskette. Im Falle des Photoperiodismus, speziell der Tageslängenabhängigkeit der Blütenbildung als seines Zentralproblems, sind so gut wie alle bisherigen Untersuchungen vom zweiten Ansatzpunkt ausgegangen, die genotypische Grundlage der untersuchten Erscheinung blieb — selbst da, wo das photoperiodische Verhalten nahe verwandter Formen, etwa verschiedener Varietäten oder Sorten einer Art, vergleichend geprüft wurde — als konstante, aber nicht näher bekannte Grösse unberücksichtigt. Die einzige Ausnahme bildet die Arbeit von BREMER (BREMER 1931, BREMER u. GRANA 1934; s. a. das Sammelreferat von ERNST-SCHWARZENBACH 1936); er untersuchte bei *Lactuca sativa* den Erbegang der photoperiodischen Reaktionsweise und fand, dass der Langtagcharakter von Winter- und Frühjahrssalaten gegenüber dem tagneutralen Charakter von Sommersalaten dominiert und dass der Unterschied monofaktoriell bedingt ist.

Für das Erreichen des oben genannten Endzieles der Arbeit, die Aufklärung der gesamten entwicklungsphysiologischen Reaktionskette, scheint es rationell zu sein, den Weg der Genotyp-Analyse mehr zu beschreiten als bisher. Die vorliegende Mitteilung soll einen Beitrag dazu liefern durch die Genanalyse der photoperiodischen Reaktionsweise einer Kurztagpflanze. Als Objekt wurde die Varietät "Maryland-Mammut" von *Nicotiana tabacum* gewählt, eine Form, die wiederholt bei der Untersuchung von Problemen des Photoperiodismus herangezogen worden ist; dies letzte ist eine Voraussetzung dafür, dass es mit Fortschreiten der Arbeit gelingen kann, die genetischen und die physiologischen Ergebnisse zu koordinieren.

Material:— Die Analyse wurde vorgenommen an Hand von Bastarden mit *Nicotiana tabacum* "Java". Die Kreuzungen wurden von Dr. G. MELCHERS hergestellt und mir zur weiteren Auswertung überlassen.

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* Aus der Botanischen Abteilung der Arbeitsstätte für Virusforschung des KWI für Biochemie und Biologie. — Reprinted, with the author's permission, from Zeitschr. Indukt. Abstamm. Vererbungsl. 80: 214-219, 1942.

Das ursprüngliche Saatgut von "Maryland-Mammut" stammt von Prof. W. W. Garner, Bureau of Plant Industry, Washington, das von "Java" von Prof. P. Koenig, Reichsinstitut für Tabakforschung, Forchheim/Baden.

Der Kurztagcharakter von *Maryland-Mammut* ist zur Genüge bekannt; an dieser Form wurde die Abhängigkeit der Blütenbildung von der Tageslänge zum erstenmal bewusst beobachtet (Garner u. Allard 1920). Die photoperiodische Reaktion trägt hier qualitativen Charakter; unter Langtagbedingungen (sowie normalen — nicht zu tiefen — Temperaturen; vgl. Roberts u. Struckmeyer 1939) bleiben die Pflanzen unbegrenzte Zeit vegetativ. Bei *Java* werden Blüten in Lang- wie in Kurztag gebildet, in Langtag jedoch etwas beschleunigt; das kommt sowohl in der Blütezeit als auch — was entscheidender ist — der Zahl der am Hauptspross vor der Blütenanlage gebildeten Internodien zum Ausdruck (Tab. 1); die Unterschiede sind statistisch gut gesichert.

Tabelle 1: *Nicotiana tabacum "Java", photoperiodisches Verhalten:*— Aussaat: 7. VI. 1941, Kultur im Gewächshaus. Temperatur durchschnittlich 20-25°. Langtag: natürlicher Tag (Juni bis September). Kurztag: 10^h Licht täglich (7^{00}-17^{00}). Individuenzahl: je 25.

	Entwicklungsdauer (Tage von der Aussaat bis zur 1. Blüte)		Zahl der Internodien am Hauptspross[1]		Sprosshöhe (dm)	
	M ± m	Variationsbreite	M ± m	Variationsbreite	M ± m	Variationsbreite
Langtag	89,0±1,0	82-100	21,2±0,5	17-25	15,28±0,23	13,0-17,5
Kurztag	97,8±1,4	91-112	25,5±0,4	23-31	10,30±0,11	9,0-11,0
Differenz	8,9±1,7	.....	4,3±0,6	....	4,98±0,25	.....

[1] Die ersten, gestauchten Internodien wurden nicht mitgezählt; ihre Zahl ist im Durchschnitt bei allen Exemplaren dieselbe.

Die Varietät ist demnach als Langtagpflanze mit quantitativer Reaktionsweise anzusprechen: der Grad der Reaktion ist jedoch gering — zwischen Langtag- und Kurztagexemplaren kommen Überschneidungen vor — und tritt gegenüber der qualitativen Reaktion von *Maryland-Mammut* so weit zurück, dass im Vergleich mit dieser Form *Java* als tagneutral bezeichnet werden kann (zur Definition und Einteilung von photoperiodisch reagierenden Pflanzen sowie zur gesamten Problemlage vgl. Lang u. v. Wettstein 1941 sowie Melchers u. Lang 1942).

Befunde:— Die Beobachtungen über die Blütenbildung der Eltern und der Bastarde unter natürlichen Tageslängenbedingungen sind zusammenfassend in Tabelle 2 zusammengestellt, der zeitliche Verlauf diagrammatisch auf Fig. 1. Bei einem Versuch wie dem vorliegenden ist es ohne Bedenken möglich, aus dem Erscheinen sichtbarer Blüten unmittelbar auf den eigentlichen Grundvorgang der Blütenbildung, d. h. auf den Übergang des Vegetationspunktes vom vegetativen Wachstum zur Ausgliederung von Blütenprimordien, zu schliessen, denn im Laufe der sommerlichen Langtage nicht zur Blüte kommende Pflanzen bilden, wie eine mikroskopische Prüfung ergibt, auch niemals Blütenanlagen aus, während die

TABELLE 2: *Nicotiana tabacum, Maryland-Mammut × Java, Vererbung der photoperiodischen Reaktionsweise:—*

Aussaat: 24. IV. 1941. Kultur im Freien (ausgepflanzt 4. VI) unter natürlichen Tagesbedingungen.

	N	Beobachtung		F_2 Erwartung 3:1			
		blühend	nicht-blühend	blühend	nicht-blühend	X^2 [1]	P (n = 1)
Java	52	52	..	.....	.....	....	.....
Maryland-Mammut..	50	..	50	.....	.....	....	.....
F_1 *M. M.* × *Java*...	50	50	..	.....	.....	....	.....
F_1 *Java* × *M. M.*...	48	48	..	.....	.....	....	.....
ΣF_1	98	98	..	.....	.....	....	.....
F_2 *M. M.* × *Java* I[2].	94	76	18	70,5	23,5	1,716	0,1—0,2
II.	93	68	25	69,75	23,25	0,176	0,5—0,7
F_2 *Java* × *M. M.* I..	92	65	27	69,0	23.0	0.926	0.3—0.5
II.	98	69	29	73,5	24,5	1,102	0,2—0,3
III	90	61	29	67,5	22,5	2,504	0,1—0,2
ΣF_2	467	339	128	350,25	116,75	1,445	0,2—0,3

Heterogenitätsprüfung:			
$\Sigma\chi^2 F_2$ I, II	6,424	(n = 5)	
$\chi^2 \Sigma F_2$	1,445	(n = 1)	
χ^2Het.	4,979	(n = 4)	p = 0,2—0,3

[1] $\chi^2 = (a_1 - 3a_2)^2$.

[2] F_2 I, II = Nachkommenschaften einzelner F_1-Individuen.

Weiterentwicklung der einmal angelegten Blüten zeitlich sehr einheitlich verläuft.

Die Befunde beweisen, dass dem Merkmalsgegensatz Kurztagcharakter (*Maryland-Mammut*) — tagneutrales Verhalten (*Java*) ein Faktorenpaar zugrunde liegt, wobei das Allel für Kurztagverhalten rezessiv ist. Die F_1 und drei Viertel der F_2-Bastarde kamen unter den natürlichen Langtagverhältnissen zur Blüte, die Blütezeit dieser F_2-Individuen deckt sich, von einzelnen Nachzüglern abgesehen, mit der Blütezeit von *Java* und der F_1. Die übrigen F_2 Pflanzen (in Tab. 2 und Diagramm als "nichtblühend" bezeichnet) blieben bis Ausgang September vegetativ; die ersten von ihnen begannen erst Anfang Oktober Knospen zu zeigen, als auch *Maryland-Mammut* mit der Knospenbildung begann. Die statistische Sicherung (Berechnung nach MATHER 1938) ist sowohl für die einzelnen Spalt-Zahlen als auch für die Homogenität befriedigend. Der Verlauf der F_2-Kurve zusammen mit der Lage der F_1 und der *Java*-Kurve macht es höchst wahrscheinlich, dass die Dominanz des Allels für tagneutrale Reaktion unvollständig ist: die F_2-Kurve ist deutlich zweigipfelig; der erste Gipfel entspricht ziemlich gut dem *Java*-Elter, d.h. den Dominant-Homozygoten, der zweite der F_1 also den Heterozygoten. Die Verschiebung des dem *Java*-Elter entsprechenden Gipfels der F_2-Kurve und die Ausziehung der ganzen Kurve nach der rechten Seite machen daneben die Mitwirkung zusätzlicher Faktoren wahrscheinlich. Bei diesen Faktoren dürfte es sich um Gene für frühere oder spätere Blütezeit handeln, die mit der photoperiodischen Reaktion nichts zu tun haben; ihre Wirkungsstärke tritt gegenüber dem Tageslängenfaktor durchaus zurück.

Der Faktor für die photoperiodische Reaktionsweise wirkt ausgesprochen pleiotrop; er beeinflusst ausser der Blütenbildung vor allem die Verzweigung der Pflanzen sowie die Wuchshöhe. Unter Langtagverhältnissen sind die — nichtblühenden — *Maryland-Mammut*-Pflanzen überhaupt nicht, die *Java*- und die F_1-Pflanzen dagegen reichlich verzweigt; dabei übertreffen bei *Java* die Seitenäste den Hauptspross im Zustand voller Blüte weit an Länge, während bei den F_1-Individuen Haupt- und Seitensprosse ungefähr gleich hoch werden. In der F_2 sind diese Bezie-

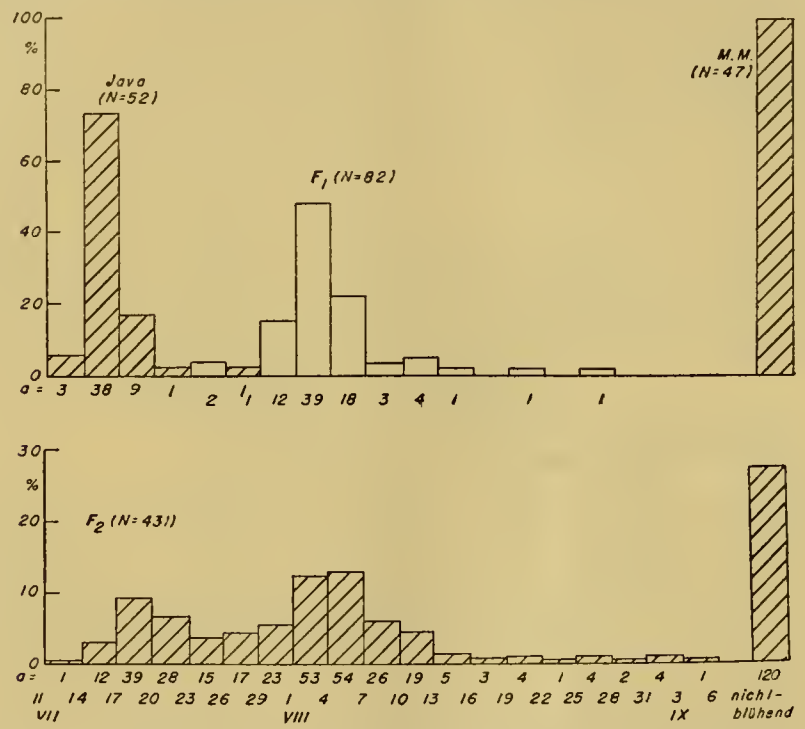

Fig. 1.—*Nicotiana tabacum Maryland-Mammut* × *Java*. Verlauf der Blüte unter natürlichen Tageslängenbedingungen.—Material entsprechend Tab. 2. Ordinate: Anzahl der aufgeblühten Individuen in %; Abszisse: Kontrolldaten. Der Ordinatenmasstab ist bei der F_2 auf das Doppelte überhöht. Unter der Abszisse sind die absoluten Individuenzahlen für die einzelnen Klassen eingetragen.

hungen gewahrt. Die Korrelation zwischen Blütenbildung und Ausbleiben derselben einerseits, Vorhandensein bzw. Fehlen der Verzweigung andererseits ist absolut; alle in Langtag blühenden Individuen sind ± reich verzweigt, alle nichtblühenden unverzweigt. Die Korrelation zwischen früherer und späterer Blüte und dem Verzweigungstyp ist weniger vollständig, aber immerhin sehr deutlich. So zeigten unter den 51 zwischen dem 15. und 20. VII. zur Blüte gekommenen F_2-Pflanzen 44 den *Java*-Verzweigungstyp, unter den 106 zwischen dem 2. und 7. VIII. zur Blüte gekommenen eine einzige.

Die Beziehungen zwischen der photoperiodischen Reaktion und der Wuchshöhe lassen sich der Fig. 2 entnehmen. In Langtag sind die blü-

henden *Java*-Pflanzen niedriger als die vegetativen *Maryland-Mammut*. Die F_1-Bastarde sind höher als beide Eltern; da die Höhe von *Maryland-Mammut* in blühendem Zustand aber unbekannt ist, lässt sich von Heterosis nicht mit Bestimmtheit sprechen. In der F_2 überwiegen unter den frühblühenden Invididuen niedrigerwüchsige Typen, unter den späterblühenden hochwüchsige; die nichtblühenden Exemplare sind aber höher als *Maryland-Mammut*. Darüber hinaus ist in allen Fällen — bei den P- und F_1-Stämmen wie in der F_2 — die Zahl der Stengelinternodien bei blühenden Exemplaren wesentlich kleiner, das einzelne Internodium demnach länger als bei den vegetativen. Die Wuchshöhe der Pflanzen ergibt sich danach aus zwei Einzelvorgängen, die Intensität des Längenwachstums, ausgedrückt durch die Länge des einzelnen Internodiums, und der zeit-

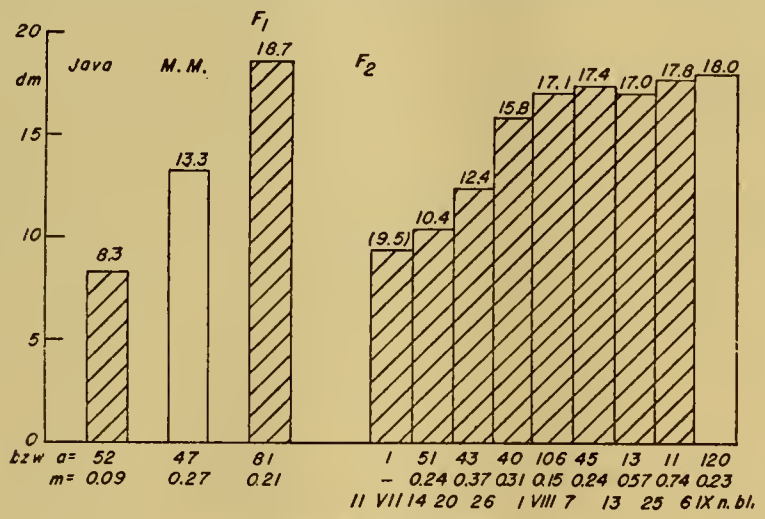

Fig. 2.—*Nicotiana tabacum Maryland Mammut* × *Java*. Wuchshöhe in Beziehung zur Blütenbildung.—Material entsprechend Fig. 1 und Tab. 2. Ordinate: Sprosshöhe in dm (Mittelwerte), für die blühenden Individuen gemessen im Zustand voller Blüte, für die nichtblühenden am 20. IX. als Stichtag: Abszisse: Blütezeiten (F_2), Individuenzahlen, mittlere Fehler.

lichen Dauer desselben. Die genotypisch-physiologische Steuerung des Merkmals dürfte folgende sein: Einmal steht es in Abhängigkeit von der Blütenbildung, also vom Tageslängenfaktor. Bei einer Allelenkonstitution, die unter Langtagverhältnissen Blütenbildung zulässt, wird die Wachstumsintensität gefördert (längere Internodien!); der Eintritt der Blütenbildung selbst führt aber zwangsläufig zur Beendigung des Längenwachstums, so dass gerade die am frühesten blühenden Pflanzen, also die Dominant-Homozygoten, am niedrigsten bleiben. Bei den Rezessiv-Homozygoten ist die Intensität des Wachstums geringer; das wird aber durch die unbegrenzte Dauer desselben unter Langtagbedingungen kompensiert und sogar überdeckt. Ausserdem müssen, wie die Höherwüchsigkeit der nichtblühenden F_2-Pflanzen gegenüber dem *Maryland-Mammut*-Elter ergibt, noch spezifische Längenwachstumsgene vorhanden sein, wobei die wirksameren Allele aus *Java* stammen müssen. Diese Gene können zum Teil auch den Hochwuchs der F_1 und der später blühenden

F_2-Bastarde mitbedingen; bei für den Tageslängenfaktor dominant-homozygoten Formen, also auch *Java* selbst, kommen sie aber nicht oder nur wenig zur Auswirkung, sind somit gegenüber diesem Faktor hypostatisch.

Diskussion:— Auf Grund der F_2-Analyse lässt sich sagen, dass das Kurztagverhalten von *Maryland-Mammut* gegenüber dem weitgehend tagneutralen Charakter von *Java* monofaktoriell-rezessiv bedingt ist; die Dominanz des tagneutralen Typs ist unvollständig. Denselben Befund machten MELCHERS u. HASSINGER-HUIZINGA (unveröff.) in Kreuzungen von *Maryland-Mammut* mit der wie *Java* tagneutralen Tabakrasse "Ambalema". Dass die "Mammut"-Typen von *Nicotiana tabacum* bei Kreuzung mit "normalwüchsigen" Formen im Verhältnis 1 : 3 spalten, und dass die F_1 leicht intermediär ist, hat bereits ALLARD (1919) gefunden. Jedoch sah er, ebenso wie alle Autoren, die solche Mammut-Typen beschrieben haben, das Riesen- oder "unbegrenzte" (indeterminate) Wachstum als das entscheidende, direkte Charakteristikum dieser Formen an. Das ist nach der vorliegenden Untersuchung nicht der Fall; entscheidend ist vielmehr das photoperiodische Verhalten derselben, während das Wachstum im wesentlichen erst sekundär mitbeeinflusst wird und auch von spezifischen Genen abhängt. Unter Kurztagbedingungen verläuft die Blütezeit aller F_2-Individuen in Form einer eingipfeligen, kontinuierlichen Variationskurve, und es treten keinerlei Mammuth-Typen auf[1]. Bemerkenswert ist, dass Mammut-Formen nicht nur bei *Maryland*-Tabaken, sondern auch bei einer ganzen Reihe anderer Tabakformen bekannt sind (vgl. HUNGER 1905, LODEWIJKS 1911, HAYES u. BEINHART 1914, HAYES 1915, ALLARD a. a. O.); die Spaltung bei Kreuzung mit Normaltypen ist in allen Fällen monohybrid, während bei Kreuzung verschiedener Mammut-Formen untereinander in der F_1 wieder der Mammut-Typ auftritt (ALLARD a. a. O.). Den Kurztagformen von *Nicotiana tabacum* liegt demnach durchweg ein und dieselbe einfache Genmutation zugrunde. Die Mutation muss ziemlich häufig sein und muss erst nach der Entstehung der — bekanntlich amphidiploiden — Art aufgetreten sein. Jedoch scheint der Kurztagcharakter nicht immer so absolut ausgeprägt zu sein wie bei *Maryland-Mammut;* es ist nicht zu entscheiden, ob es sich dabei um verschieden starke Allele des Tageslängenfaktors oder um einen Einfluss des Restgenotyps handelt.

Durch Aufpfropfung von Reisern von *Java* und ebenso von anderen tagneutralen Rassen, z. B. "Samsun", gelingt es, *Maryland-Mammut*-Pflanzen unter Langtagbedingungen zur Blüte zu bringen, wenn auch weniger gut als mit qualitativ reagierenden Langtagformen (s. MELCHERS u. LANG 1941, MOŠKOV 1937). Der Mechanismus der Auslösung der Blütenbildung ist fraglos stofflicher Natur; am ehesten ist dabei an spezifische, hormonartige Stoffe zu denken, wenn auch ein stichhaltiger Nachweis durch Reingewinnung dieses "Blühhormons" (oder dieser Blühhormone) bisher nicht gelungen ist und auf grosse methodische Schwierigkeiten stösst. Es wäre aber verfehlt, das dem Kurztagverhalten von *Maryland-Mammut* zugrunde liegende Gen (bzw. sein dominantes Allel) in direkte Beziehung zur Blühhormonproduktion zu setzen, und das Blüh-

[1] Die Aufzucht dieser Pflanzen erfolgte in Töpfen unter Verdunkelungsvorrichtungen; ein direkter Vergleich von Blütezeit und Grössenmassen mit den im Freiland gezogenen Langtagkulturen ist deshalb nicht möglich.

hormon als Genwirkstoff zu bezeichnen. Bei seinen Untersuchungen über die Blühreife von *Hyoscyamus niger* hat MELCHERS (1937) die gleiche Auffassung vertreten; er lehnte es ab, die durch Pfropfversuche zwischen ein- und zweijährigen Formen wahrscheinlich gemachte Produktion von Blühhormonen mit dem für den Erbunterschied zwischen diesen Formen verantwortlichen Gen unmittelbar in Verbindung zu bringen und warnte allgemein, auf Grund von Parallelen zwischen Gen- und stofflichen Wirkungen zu enge, direkte, Zusammenhänge zwischen Gen und Wirkstoff anzunehmen. Im Falle photoperiodische Reaktion — Blühhormonbildung ist diese Auffassung noch näherliegend, weil einige spezielle Hinweise dafür vorhanden sind, dass beide Vorgänge nicht in unmittelbarer, kausaler Beziehung zueinander stehen. Bei *Hyoscyamus niger,* einer Langtagpflanze, scheint die photoperiodische Reaktion eine sekundäre Hemmungsreaktion zu sein, während die unmittelbaren, primären Prozesse der Blütenbildung tageslängenunabhängig sind (LANG u. MELCHERS 1941, LANG 1941); die Blühhormonbildung wird man dann eher mit diesen zweiten, tageslängenunabhängigen Primärvorgängen der Blütenbildung in Verbindung bringen. Wie die entsprechenden Verhältnisse bei Kurztagpflanzen liegen, ist derzeit nicht zu entscheiden (vgl. a. LANG u. v. WETTSTEIN 1941, MELCHERS u. LANG 1942); die Möglichkeit, im Transplantationsexperiment bei Kurztagpflanzen Blütenbildung durch Langtagformen auszulösen, und auch umgekehrt (eigenes Material, unveröff.), beweist aber in jedem Fall, dass die Blühhormone von Lang- und Kurztagpflanzen entweder identisch sind oder doch in ihrer Genese und Wirkung eng zusammenhängen. Bei dieser Sachlage ist es m. E. ganz allgemein verfrüht, einzelne Gene bereits ganz bestimmten Einzelprozessen im Rahmen der Gesamtvorgänge der Blütenbildung zuzuordnen; dazu sind weitere Untersuchungen — physiologische wie genetische — erforderlich.

Besonders interessant und auch für die Frage ihrer gegenseitigen physiologischen Stellung aufschlussreich wäre es, das genotypische Verhältnis von ausgesprochenen, qualitativ reagierenden, Lang- und Kurztagpflanzen zu untersuchen. Auffallenderweise scheint es jedoch solche Formen innerhalb engerer, unbegrenzte Bastardierung zulassender Verwandtschaftskreise nebeneinander nicht zu geben, sondern immer nur entweder tagneutrale und Langtagformen, oder tagneutrale und Kurztagtypen. Das zusammen mit der Tatsache, dass das Kurztagverhalten gegenüber dem tagneutralen rezessiv, der Langtagcharakter nach den eingangs zitierten Untersuchungen BREMERS an *Lactuca sativa* dagegen dominant ist, deutet darauf, dass der Gegensatz zwischen den beiden Reaktionstypen auf mehr als einem einzelnen Faktor beruht. Es wird versucht, die Frage durch Kreuzungen zwischen *Maryland-Mammut* und der Langtagart *Nicotiana silvestris* zu klären. In der F_1 erweist sich nach den bisherigen Beobachtungen der Langtagcharakter von *silvestris* als absolut dominant. Durch Rückkreuzung der — hochgradig sterilen — Bastarde mit *Maryland-Mammut* und anderen Tabakformen, evtl. auch auf dem Weg über amphidiploide Formen, lässt sich vielleicht ein echter Langtag-Tabak gewinnen, mit dem die gewünschte Analyse durchgeführt werden kann.

Zum Abschluss sei noch kurz zu einer Frage im Zusammenhang mit der pleiotropen Wirkung des Tageslängenfaktors auf die Verzweigung Stellung genommen. Als Mechanismus bei der engen korrelativen Bezie-

hung zwischen Verzweigung und Blütenbildung wird vor allem an eine Beteiligung von Wuchsstoffen zu denken sein. Dass das Austreiben von Seitensprossen durch Wuchsstoff verhindert wird, ist erwiesen (THIMANN u. SKOOG 1933, 1934); ob die Wirkung direkt oder indirekt erfolgt, ist allerdings stark umstritten (vgl. die Zusammenfassungen bei WENT u. THIMANN 1937, Kap. XII, und THIMANN 1939, ferner WENT 1939, SKOOG 1939 sowie SNOW 1940 und dort zitierte Literatur). Eine Beteiligung von Wuchsstoffen an den Gesamtvorgängen der Blütenbildung ist mit Gewissheit anzunehmen, da dabei Streckungsvorgänge eine grosse Rolle spielen, und zwar nicht nur der eigentlichen Blütenorgane, sondern — vor allem bei Langtagpflanzen, deren Achse im vegetativen Zustand gewöhnlich rosettig gestaucht bleibt — auch der Achsenteile; die Art der Beziehungen im einzelnen ist aber noch ganz unbekannt. Nach den Beobachtungen an den *Maryland-Mammut-Java*-Bastarden ist in erster Linie zweierlei denkbar. Einmal könnte das Ausbleiben der Blütenbildung ebenso wie das Fehlen der Verzweigung durch zu hohe Wuchsstoffkonzentrationen bewirkt sein; der Wuchsstoff würde dann beide Vorgänge direkt oder indirekt, aber gleichsinnig und aktiv beeinflussen. Zum anderen ist es denkbar, dass bei der Weiterentwicklung der angelegten Blüten grössere Wuchsstoffmengen verbraucht würden und die übrigen Teile der Pflanzen dadurch weniger Wuchsstoff erhielten, und dass auf diese Weise die Hemmung der Seitenknospen fortfiele; Verzweigung und Blütenbildung würden dann passiv zusammenhängen und ihre Beziehung wäre im Grunde gegensinnig. A priori liegt die zweite Möglichkeit näher, denn eine aktive, determinierende Funktion von Auxinwuchsstoffen beim Übergang der Pflanze vom vegetativen Wachstum zur Blütenanlage ist sehr unwahrscheinlich, zum mindesten (vgl. ČAJLAHJAN u. ŽDANOVA 1938*a-c*) liegen keinerlei Anzeichen dafür vor (eine gewisse, wohl durchaus unspezifische Hemmwirkung von Wuchsstoff auf die Blütenbildung scheint in manchen Fällen zu existieren; vgl. z. B. HAMNER u. BONNER 1938, S. 416, ČAJLAHJAN u. ŽDANOVA 1938*c*). Geklärt werden können die hier angeschnittenen Fragen wieder nur durch weitere Versuchsarbeit; da experimentelle Beiträge in der Richtung noch gänzlich fehlen, dürften solche Untersuchungen lohnend sein.

Zusammenfassung:— Die genische Grundlage der Tageslängenabhängigkeit der Blütenbildung bei der Varietät "Maryland-Mammut" von *Nicotiana tabacum* wurde in Kreuzungen mit der weitgehend tagneutralen Rasse "Java" untersucht. Der Kurztagcharakter von *Maryland-Mammut* erwies sich als monofaktoriell bedingt und rezessiv, bei unvollständiger Dominanz des Allels für tagneutrales Verhalten.

Das Vorkommen von durch denselben Faktor bedingten Kurztagformen bei einer ganzen Reihe von Tabakrassen zeigt, dass die Kurztagreaktion in der Art auf einer einzelnen, einfachen, mit relativ grosser Häufigkeit auftretenden Genmutation beruht.

Die Wirkung des Faktors ist pleiotrop; ausser der Blütenbildung werden Verzweigung und Längenwachstum betroffen; besonders für das Längenwachstum sind ausserdem auch andere, spezifische Gene vorhanden, die gegenüber dem Tageslängenfaktor hypostatisch sind.

Die Befunde werden kurz im Zusammenhang mit einigen Fragen des Photoperiodismus und der Blütenbildung allgemein besprochen.

Die Arbeit wurde im Rahmen der "Untersuchungen über die Genetik und Entwicklungsphysiologie der Blühreife" (Dr. G. MELCHERS) durchgeführt; diese Untersuchungen werden vom Reichsforschungsrat unterstützt. An der Aufnahme und Auswertung des Materials haben Fräulein U. WOELFFER und Fräulein H. KUNISCH wesentlichen Anteil; die Pflege der Kulturen wurde von Garteninspektor H. JENKE und dem Gartenpersonal des KWI für Biologie besorgt.

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Nachtrag: Genetik der Vernalisation und des Photoperiodismus: — Die überwiegende Mehrzahl der Untersuchungen über Vernalisation und Photoperiodismus sind physiologischer Art. Die genotypische Basis der untersuchten Erscheinungen blieb als konstante, aber nicht näher bekannte Grösse unberücksichtigt, und zwar auch da, wo Formen verschiedenen Genotyps, z.B. Rassen der gleichen Art, vergleichend untersucht wurden. Die Vernachlässigung der genetischen Seite des Problems ist zweifellos zu bedauern, denn wie mehrere Beispiele der letzten Jahre, u.a. die Untersuchungen über die Genetik und Physiologie der Augenfarbstoffe bei Insekten und über die Biosynthese verschiedener biologisch bedeutsamer Verbindungen bei *Neurospora* beweisen, kann gerade die Kombination genetischer und physiologischer Untersuchungen die Arbeit besonders erfolgreich machen. Ueberdies sind von einer eingehenderen genetischen Analyse von Vernalisation und Photoperiodismus auch neue Gesichtspunkte zum Verständnis der beiden Erscheinungen zu erwarten. Denn auch die gegenseitigen physiologischen Beziehungen zwischen den verschiedenen Reaktionstypen, den Zweijährigen und Winterannuellen einerseits[1], den Lang- und Kurztagpflanzen andrerseits, sind noch nicht in jeder Hinsicht klar; z.B. wissen wir nicht, ob die photoperiodischen Reaktionen der Lang- und der Kurztagpflanzen auf ganz verschiedenen Vorgängen beruhen, oder ob einige der daran beteiligten Vorgänge bei beiden Reaktionstypen die gleichen sind. Gelänge es, das genetische Verhältnis dieser beiden Typen zueinander festzustellen, so liessen sich wahrscheinlich auch Rückschlüsse auf das physiologische gewinnen.

Die wenigen bisher vorliegenden Untersuchungen lassen solche Rückschlüsse noch keineswegs zu. Sie beschränken sich auf die Analyse der genetischen Unterschiede *1.* zwischen Zweijährigen oder Winterannuellen und einjährigen Sommerannuellen, *2.* zwischen Lang- oder Kurztagpflanzen einerseits und Tagneutralen andrerseits; die Typen mit ausgesprochener Reaktionsweise werden also nicht miteinander verglichen, sondern mit Formen, denen solch ausgesprochene Reaktion auf Kälte- oder Tageslängeneinwirkung fehlt.

Für Zweijährige liegen, soweit der Verf. übersieht, nur Untersuchungen an *Hyoscyamus niger* und an der Zuckerrübe vor. Bei *Hyoscyamus* ist der Unterschied zwischen ein- und zweijähriger Entwicklungsweise durch ein mendelndes Gen bedingt, und die Zweijährigkeit ist dominant (8, 24). Correns hielt die Dominanz für vollständig; Melchers fand aber, dass Heterozygote bei früher Aussaat häufig schon im ersten Jahr

[1] In der floristischen und ökologischen Literatur scheinen die Begriffe einjährig und winterannuell nicht einheitlich verwendet zu werden. Als zweijährig sollten solche Pflanzen bezeichnet werden, die ohne Vernalisation überhaupt nicht zur reproduktiven Entwicklung kommen, als winterannuell (Winterformen) solche, bei denen die Blütenbildung durch Vernalisation zwar beschleunigt wird, nach Ablauf einer gewissen Entwicklungszeit aber auch ohne diese, gleichsam zwangsläufig, eintritt. Es gibt allerdings unter den jetzt zu den Zweijährigen oder den Winterannuellen gestellten Formen viele, deren Zugehörigkeit zu der einen oder der anderen Gruppe noch geprüft werden muss.

zur Blütenbildung kommen, dass die Dominanz also unvollständig ist. Bei der Zuckerrübe fand MUNERATI (26) in Kreuzungen zwischen einer Rasse mit starker Tendenz zum Schossen im ersten Jahr und mehreren wie üblich zweijährigen Rassen dagegen zwar ebenfalls deutliche monogene Vererbung, aber Dominanz der Einjährigkeit, während einige ältere Autoren kompliziertere Ergebnisse hatten (9, 14).

Die Untersuchungen an Winterannuellen sind zahlreicher, wenn sie sich auch ausschliesslich auf Getreide beschränken. Die Ergebnisse sind je nach den zur Kreuzung verwendeten Sorten recht verschieden. In der Mehrzahl der Fälle wurden in der F_1 vollständige Dominanz des Sommertyps und in der F_2 eine monogene Spaltung gefunden. Dafür gibt es Beispiele für Weizen (7, 27), Gerste (34) und Roggen (30), während für Hafer überhaupt noch keine Analysen zur Genetik des Sommer- und Wintertyps vorliegen. Auch SCHIEMANN (32) fand bei Gerste eine Spaltung in 75% Sommer- und 25% Wintertypen; ob die Dominanz vollständig war, ist der Arbeit nicht zu entnehmen, da F_2, F_1 und P-Formen nicht unmittelbar miteinander verglichen wurden. Monogene, aber intermediäre Vererbung, also eine F_2-Spaltung von 1 : 2 : 1, geben SPILLMAN (33) und OLSON *et al.* (28) bei Weizen bzw. Weizen und Gerste an; vielleicht lassen sich auch die Ergebnisse von BIFFEN (3) und von VAVILOV u. KUZNECOVA (36) ebenso deuten. Dominanz des Wintertyps fand TSCHERMAK (35) bei Roggen. Die Spaltung in einer der Kreuzungen entspricht dem monogenen Verhältnis, die gefundenen Zahlen sind aber nicht verlässlich, da die F_1-Pflanzen gegen Kreuzung (Bestäubung) ausser mit ihresgleichen nicht gesichert waren und Roggen bekanntlich ausgesprochener Fremdbefruchter ist.

Es ergibt sich somit bei Zweijährigen wie bei Wintergetreiden ein auf den ersten Blick sehr widerspruchsvolles Bild: in manchen Kombinationen ist der zweijährige oder der Wintertyp dominant, in anderen der einjährige oder der Sommertyp; beim Wintertyp–Sommertyp scheint es auch intermediären Erbgang zu geben. Es ist allerdings möglich, alle bisher besprochenen Fälle einheitlich zu deuten, und zwar mit der Annahme von zwei Genen (Allelenpaaren): einem "Grundgen", welches den Unterschied zweijährig–einjährig oder Wintertyp–Sommertyp bedingt, wobei das Allel für Zweijährigkeit oder Winterverhalten dominant ist, und einem Inhibitor, dessen dominantes Allels die Wirkung dieses Grundgens aufhebt. Eine dahingehende Annahme hat erstmalig COOPER (7) gemacht; neuerdings ist sie wieder von PURVIS (30) erörtert worden. Zweijährige oder Winterformen hätten nach dieser Annahme die genetische Konstitution Wi, einjährige und Sommerformen können WI, wI oder wi sein. Hat der zur Kreuzung verwendete einjährige oder Sommer-Elter die Formel wi, so ergibt sich "Dominanz" des zweijährigen oder des Wintertyps, hat er wI, so ergibt sich "Dominanz" des einjährigen bzw. des Sommertyps. Dafür, dass diese Deutungsmöglichkeit Beachtung verdient, sprechen die Tatsachen, dass in manchen Kreuzungen zwischen Winter- und Sommerweizen zwar Dominanz des Sommertyps, aber eine F_2-Spaltung von 13 : 3 vorzukommen scheint (7), während aus Kreuzungen bestimmter Sommerformen von Gerste Wintertypen im Verhältnis 3 : 13 herausspalten sollen (11). Jenes ist zu erwarten, wenn eine Winterform

mit einem Sommertyp der Formel WI gekreuzt wird, dieses bei Kreuzungen von Sommerformen der Konstitution WI und wi.

Es gibt jedoch weitere Fälle, in denen die Zahl der beteiligten Gene zwar nicht bestimmt werden konnte, aber wahrscheinlich grösser als 1–2, und ihre Wirkung kumulativ ist (z.B. 1, 12, 15–17, 22). Das skizzierte Schema kann also keineswegs als gesichert und allgemein gültig angesprochen werden. Allerdings sprechen, das muss hervorgehoben werden, solche komplizierteren Fälle nicht unbedingt gegen eine grundsätzlich einfache genetische Basis des Unterschiedes Winter- gegen Sommerform. Auch in fast allen Fällen, in denen eine mehr oder minder klare und einfache Spaltung gefunden wurde, war der Variationsbereich der Blütezeiten in der F_2 oder den F_2-Klassen gegenüber den P-Formen und der F_1 vergrössert, d.h. es waren weitere die Blütenbildung beeinflussende Gene beteiligt. Diese Gene brauchen nicht notwendigerweise etwas mit dem Unterschied Winterform–Sommerform zu tun zu haben, z.B. kann es sich um Gene handeln, die die Vegetationsdauer schlechthin beeinflussen. Wird der Einfluss derartiger Gene relativ stärker, so können sie die Wirkung der Gene für Sommer- oder Winterverhalten überdecken und dadurch auch für dies Merkmal einen komplizierten Erbgang vortäuschen. Hinzu kommt eines: die meisten Kreuzungen zwischen Winter- und Sommergetreiden wurden noch ohne Kenntnis des Wesens des physiologischen Unterschiedes der beiden Reaktionstypen, d.h. des "Kältebedürfnisses" der Winterannuellen (Gassner, 13), und damit der eigentlichen Grundlage der Vernalisation, oder ohne nähere Beachtung dieser Kenntnis ausgeführt. Infolgedessen wurde die Möglichkeit einer modifikativen Beeinflussung in der Ausprägung des Wintertyps, die sehr gross sein kann (z.B 17), nicht oder nicht genügend berücksichtigt, und in manchen Fällen dürften phänotypische Variationen die genotypischen Differenzen überlagert haben. Nicht berücksichtigt wurde auch, dass der Unterschied zwischen Winter- und Sommerformen gleitend ist; für die Kreuzungen wurden mehr oder weniger zufällige Sorten herausgegriffen, ohne dass bekannt gewesen wäre, ob es sich um scharf ausgeprägte Winter- bzw. Sommertypen handele. Würden solche Typen für die Analyse verwendet, und könnte sie, was allerdings aus technischen Gründen meist unmöglich sein wird, unter konstanten Aussenbedingungen ausgeführt werden, so dürfte das komplizierte bisherige Bild des genetischen Verhältnisses von Winter- und Sommerannuellen einfacher werden.

Auf dem Gebiete des Photoperiodismus liegen für Langtagpflanzen Untersuchungen von Bremer (4) und Bremer u. Grana (5) und von Ross (31) vor. Die erstgenannten Autoren fanden, dass der Langtagcharakter von Winter- und Frühjahrssalaten (*Lactuca sativa*) gegenüber dem tagneutralen Verhalten von Sommersalaten dominiert und dass der Unterschied auf einem Gen beruht. Ross gibt dasselbe für den Langtagcharakter einer ausgesprochenen Langtagrasse von *Epilobium hirsutum* bei Kreuzung mit einer tagneutralen, vielleicht sogar schwachen Kurztagcharakter aufweisenden anderen Rasse an; da aber die Auszählung der Aufspaltung an einem einzigen Datum (als die Langtagrasse gerade voll erblüht war) vorgenommen wurde und eine grössere Anzahl der als "nichtblühend" klassifizierten Individuen zu diesem Zeitpunkt Knospen besassen, scheint dieser Schluss noch nicht ganz sicher. Die genetische Differenz

von Kurztag- gegenüber tagneutralem Verhalten untersuchten LITTLE *et al.* (23) bei *Tagetes* und LANG* (19) bei Tabak (Sorten Maryland-Mammut und Java). Beidemal wurde monogener Erbgang, aber Dominanz des tagneutralen Verhaltens nachgewiesen. Die Dominanz ist wenigstens beim Tabak sicher unvollständig. Die Ergebnisse beim Tabak stehen in Einklang mit denen älterer Kreuzungsanalysen mit sog. Mammut-Formen, welche bei mehreren Tabakrassen bekannt sind. Auch hier wurden monogene Spaltung und unvollständige Dominanz des Normalwuchses beobachtet, während bei Kreuzung verschiedener Mammut-Formen untereinander in der F_1 Mammut-Typ auftritt (2). Der Mammut- ("indeterminate") Wuchs ist aber ein durchaus sekundäres Merkmal, bedingt durch das Ausbleiden der Blütenbildung in Langtag. In Kurztagbedingungen tritt in der F_2 von Kreuzungen zwischen Mammut- und Normaltypen kein Mammutwuchs in Erscheinung (19).

Fragt man, an welchem Punkt der Vernalisations- bzw. der photoperiodischen Vorgänge die bisher erfassten Gene eingreifen, so lässt sich eine sichere Antwort noch nicht geben. Durch Aufpfropfung einjähriger Pflanzen auf nicht-vernalisierte zweijährige und ebenso von blühfähigen Partnern auf in nicht-induktiver Tageslänge gehaltene Kurz- und Langtagpflanzen werden die für sich allein nicht blühfähigen Partner zur Blütenbildung veranlasst (6, 18, 24 u.v.a. und eigene unpubl. Versuche). Dies wird allgemein als Beweis für das Vorhandensein von Blühhormonen aufgefasst, und es liegt dann auf den ersten Blick nahe anzunehmen, dass die für das ein- oder zweijährige Verhalten oder für die photoperiodische Reaktion verantwortlichen Gene die Synthese der Blühhormone steuern. Voraussetzung für solche Deutung wäre es aber, dass die für die Vernalisation bzw. die phytoperiodische Reaktion massgebenden Vorgänge in unmittelbarer Beziehung zur Blühhormonbildung stehen, dass also die Kälte bei Zweijährigen und die induktive Tageslänge bei photoperiodisch empfindlichen Pflanzen direkt in die Vorgänge der Blühhormonproduktion eingreifen. Diese Voraussetzung ist nicht erfüllt, im Gegenteil, es gibt wenigstens im Falle des Photoperiodismus einige Hinweise, dass die Beziehung zwischen den Vorgängen keine so einfache ist. Nach den Vorstellungen von LANG u. MELCHERS (21) beruht die photoperiodische Reaktion der Langtagpflanzen darauf, dass irgendwelche Substanzen, die für die Auslösung der Blütenbildung, vielleicht für die Synthese des dazu notwendigen Blühhormons, erforderlich sind, in zu langen Dunkelphasen durch sekundäre Vorgänge wahrscheinlich dissimilatorischen Charakters abgebaut werden und die Blütenbildung auf diese Weise verhindert wird. Die Beziehung zwischen photoperiodischer Reaktion und Blüten-, speziell Blühhormonbildung wäre dann indirekter Art. Trifft das zu, so wird man ein für die photoperiodische Reaktion der Langtagpflanzen verantwortliches Gen eher mit diesen sekundären Vorgängen als mit der Blühhormonsynthese in Beziehung bringen. Da es in Pfropfversuchen auch möglich ist, ausgesprochene Lang- und Kurztagpflanzen wechselseitig zur Blütenbildung zu veranlassen (MELCHERS u. LANG, 25 und unpubl.), die Blühhormone beider Reaktionstypen also offenbar identisch sind oder wenigstens in ganz naher Beziehung zueinander stehen, gilt diese Einschränkung auch für die Kurztagpflanzen. Im Falle der Zweijährigen ist die Situa-

* *Editor's Note:* This Symposium, pp. 175-183.

tion zwar noch ganz offen; eine unmittelbare Koordinierung der zweijähriges Verhalten bestimmenden Gene und der Blühhormonbildung ist aber, worauf MELCHERS (24) bereits 1937 hinwies, *per analogiam* keineswegs von vornherein als sicher anzunehmen.

Der weiteren genetischen Analyse von Vernalisation und photoperiodischem Verhalten steht eine wesentliche Schwierigkeit im Wege: es scheint innerhalb ein und derselben Art weder eindeutige zweijährige und Winterformen, noch vor allem ausgesprochene Lang- und Kurztagpflanzen nebeneinander zu geben, sondern immer nur entweder Zweijährige und Einjährige, oder Winter- und Sommerannuelle, oder Langtagpflanzen und Tagneutrale, oder Kurztagpflanzen und Tagneutrale. Das macht ein direkte Analyse des Unterschiedes dieser Reaktionstypen zunächst unmöglich, und man kann nur hoffen, über Artkreuzungen zum Ziele zu kommen. Bei *Nicotiana* wurden solche Versuche vom Verf. begonnen, konnten aber infolge äusserer Umstände bisher nicht weitergebracht werden; in der F_1 der Kurztagpflanze *Nic. tabacum* Maryland-Mammut und der Langtagpflanze *Nic. silvestris* erwies sich der Langtagcharakter als dominant, während in der F_1 von *Nic. silvestris* und der tagneutralen *Nic. tomentosa* seine Dominanz nicht so vollständig war und individuelle Schwankungen auftraten, vielleicht allerdings nur deshalb, weil sich die Pflanzen zu nahe an ihrer kritischen Tageslänge befanden (in diesem Tageslängenbereich ist die individuelle Variation im photoperiodischen Verhalten relativ gross; s. 21). Die Tatsache, dass innerhalb eines engen Verwandtschaftskreises Formen mit gegensätzlicher Reaktionsweise nicht vorkommen, kann aber *per se* bedeutsam sein. Zusammen mit dem gegensätzlichen Dominanzverhalten in Kreuzungen von Lang- und von Kurztagpflanzen mit Tagneutralen deutet sie darauf hin, dass die beiden Typen sich genetisch stärker unterscheiden als nur durch ein Gen — ein Umstand, welcher auch mit gewissen auf rein physiologischer Grundlage gewonnenen Vorstellungen (21) in Einklang stehen würde.

Das photoperiodische Verhalten von experimentell hergestellten Autotetraploiden einer Langtagpflanze (*Hyoscyamus niger*), einer Kurztagpflanze (*Xanthium strumarium*) und zweier Tagneutraler (*Hyoscyamus albus, Antirrhinum majus*) im Vergleich mit den diploiden Stammformen wurde von LANG (20) untersucht. In einigen Fällen war die Blütenbildung verzögert, in anderen unbeeinflusst; bei *Hyoscyamus niger* war die kritische Tageslänge verschoben; die Unterschiede waren aber durchweg quantitativer Art und absolut wie relativ sehr geringfügig. Damit werden einige gegenteilige Angaben, die das Auftreten einer neuartigen photoperiodischen Reaktionsweise mit Erreichung der 4n-Stufe behauptet hatten (10, 29), zum Teil an demselben Material, widerlegt. Sie beruhen auf Nichtbeachtung photoquantitativer Effekte und Beobachtung unter zu wenig variierten Bedingungen, nämlich in nur einer Tageslänge.

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